A review of the Mastacembeloidei, a suborder of synbranchiform teleost fishes
Part II: Phylogenetic analysis

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Synopsis

The Mastacembeloidei or spiny eels (comprising the families Mastacembelidae, Chaudhuriidae and Pillaiidae) is a distinctive group of about 70 freshwater species with a tropical and subtropical Oriental and Ethiopian distribution, currently recognised as a suborder of the perciform fishes. The majority of its 70 species have been placed in a single genus, *Mastacembelus*, without regard to their genealogical relationships, and the suborder as a whole has never been the subject of a detailed taxonomic or anatomical review. A revision of the genera and families within the suborder, and a reconsideration of its interrelationships within the Percomorpha, are the overall objectives of this study.

It is based on numerous anatomical characters drawn from the descriptions in Travers (1984) and involves a comparison of their condition with that of their homologues in other teleostean lineages. This analysis indicates that the mastacembeloids, long associated with the Perciformes, should be reallocated to the Synbranchiformes. A phylogenetic hypothesis of their intrarelationships is also proposed, *viz.*, the Mastacembeloidei can be resolved into two lineages: the Chaudhuriidae (expanded to incorporate two genera) and the Mastacembelidae (divided into two subfamilies representing the Asian and African species). This hypothesis results in the elevation of the sole endemic Chinese species, *Mastacembelus sinensis,* to a monotypic genus within the Chaudhuriidae, and the generic synonymy of *Pillaia* (and *Garo*) with *Chaudhuria* (but the retention of both the latter taxa as subgenera of *Chaudhuria*). The Asian mastacembelid subfamily, Mastacembelinae, retains the genera *Mastacembelus* and *Macrognathus* although the former is restricted to six species only, and the latter expanded to include eight species previously included in *Mastacembelus.* The African species are shown to be phyletically distinct and to warrant the creation of a new subfamily and new genera for two major African sublineages.

Introduction

The Mastacembeloidei, or spiny-eels, are a group of freshwater teleost fishes occurring in the Oriental and Ethiopian zoogeographical regions. The Oriental species are widely distributed in SE. Asia and extend from the eastern China seaboard, through the continental islands of Indonesia to the Middle East (Fig. 1). This pattern, together with their recent discovery in southern Iran (Coad, 1979), gives these fishes a continuous distribution throughout their Oriental range. The absence of mastacembeloids from the Arabian Peninsula, North Africa and the Horn of Africa, however, has resulted in the geographical isolation of the Oriental fauna from the Ethiopian species. These are restricted to tropical and subtropical waters of Central Africa; embracing the Nilo-Sudan, Upper and Lower Guinea, Zaire, East Coast and Zambezi ichthyofaunal provinces of Roberts (1975).

Mastacembeloids occur in a variety of freshwater habitats at high and low altitudes, and are common in riverine and lacustrine environments, streams and ponds (Job, 1941; Sufi, 1956; Matthes, 1962; Poll & Matthes, 1962; Skeleton, 1976).

At least four African species are cavernicoles (Poll, 1953, 1958, 1959 & 1973 and Roberts & Stewart, 1976) and show considerable atrophy of the eye tissues, an associated hypertrophy of the superficial parts of the *adductor mandibulae* musculature and even lack of pigment (Poll, 1973). A group of Asian mastacembeloid taxa exhibit an elaborate burrowing mechanism (Job, 1941; Sufi, 1956); however, this habit is not found in all species (Schofield, 1962).

Most mastacembeloids appear to be carnivores with a wide range of feeding strategies. Food organisms range from small zooplankton (Job, 1941; Sufi, 1956) through aquatic insect larvae and oligochaetes (Roberts, 1980) to other fishes (pers. obs.) including both eggs and fry (Hamid Khan, 1934) and even mastacembeloid species with a relatively small adult size (Staeck, 1976). To a large extent the prey species are related to the size and developmental stage of the predators.

Reproduction in the mastacembeloids is poorly known. There are brief descriptions of the spawning activity in a single species in captivity (Schoenebeck, 1955; Polder, 1963; Franke, 1965), artificially induced spawning (Kochetov, 1982) and the periodic occurrence of vast numbers of juveniles in Lake Tanganyika (Brichard, 1978), but reproductive behaviour in nature has never been observed.

Many mastacembeloids are thought to have some form of aerial respiration (Dobson, 1874; Day, 1877; Ghosh, 1933; Hora, 1935), although reports are contradictory and the presence of suprapharyngeal or swimbladder adaptations has never been shown. Whether survival in oxygen deficient waters is by some form of cutaneous respiration (Mittal & Datta Munshi, 1971), or by inanition with respiration at a standstill (Job, 1941), requires further research before an accurate assessment can be made.

Fig. 1 Present-day distribution of mastacembeloid Oriental and Ethiopian species.

A pseudobranch, once thought to be absent in mastacembeloids (Day, 1889; Boulenger, 1915: 12) has recently been described in some Asian species (Bhargava, 1953). A spherical sac-like pseudobranch situated above the epithelium roofing the oral cavity was found in all taxa examined.

This study is based on the many osteological and myological features shown (Travers, 1984) to be of potential value in reconstructing phylogenetic relationships. These morphological characters will be analysed by comparing their condition with that of their homologues (Patterson, 1982*b*) in other groups of percomorph fishes (acanthomorphs) or with the teleosts as a whole (see below).

The objectives of these comparative studies, besides providing an analysis of mastacembeloid interrelationships with other percomorph fishes, was an attempt to revise the intrarelationships of the group. Only by revealing the phylogeny of these fishes can an improved understanding of their biogeographical history be gained (Greenwood, 1983).

Although numerous specific features were identified (see Travers, 1984), and are included where possible in the analysis, a formal species level revision was not attempted.

Materials and methods

Materials

The bulk of the comparative outgroup material examined is tabulated in Travers (1981). In addition to these specimens further taxa are listed in systematic order in Table 1; all are given with their register number and codes indicating the type of examination or preparation involved. Unless otherwise indicated, all are BM(NH) registered specimens.

For a complete list of the mastacembeloid specimens upon which this study is based, for nomenclatural references and the techniques of morphological analysis, see Travers, 1984.

Methods

The inter- and intrarelationships of the mastacembeloids were evaluated by the application of a cladistic methodology as originally defined by Hennig, 1950 & 1979 and advocated latterly by Eldredge & Cracraft, 1980, Nelson & Platnick, 1981, and Wiley, 1981. This methodology has, over the last decade, brought increased order to the complexities of teleostean classification regardless of the vociferous debate (e.g. see *Nature* Correspondence from volume **275** to **292**), and the proliferation of conceptual literature (e.g. see *Systematic Zoology* from 1967 (4): 289–292, to date), that it has engendered.

To determine the primitive (plesiomorphic) or derived (apomorphic) nature of mastacembeloid characters, in the absence of a complete ontogenetic history of all species, a series of outgroup comparisons was made in a manner similar to that discussed by Watrous & Wheeler (1981); see Farris (1982) for a critical review of their study. Information from ontogenetic transformations (de Beer, 1958; Gould, 1977; Nelson, 1978; Rosen, 1982), where available was utilized especially if comparisons could be made with similar developmental stages in outgroup taxa (Fink, 1982; Patterson, 1983).

Only those uniquely derived features confined to individuals of a single species were identified as autapomorphic characters. When detected in this restricted sense these characters can be used to identify species, regardless of whether or not they are strictly definable (Patterson, 1982*a*).

Where an outgroup has been the subject of a recent study, highly derived species were excluded so as not to be mislead by taxa that are unrepresentative for their group as a whole. In poorly studied assemblages a wide range of representatives was examined in order to avoid overlooking a group which may be masked by a previous incorrect assessment of its characters and hence given an erroneous taxonomic allocation.

Outgroup taxa were taken from all major percomorph assemblages. Emphasis was given to perciform lineages, since these represent the largest acanthopterygian groups, and several beryciform families since the perciforms are generally thought to have been derived from a beryciform species (Patterson 1964; Greenwood *et al,* 1966; McAllister, 1968; Zehren, 1979). However, these beryciform taxa are ill-defined and thought by most authors to represent polyphyletic assemblages (Patterson, 1964; Greenwood *et al,* 1966; Rosen, 1973; Zehren, 1979). Furthermore, the task of analysing such groups is complicated by the large number of taxa involved and also, as Rosen (1973: 398) observed, by: '. . . the lack of co-ordinated comprehensive studies of character complexes throughout the group'. For example, the only synapomorphy so far proposed for the Perciformes is the presence of an interarcual cartilage (Rosen & Greenwood, 1976) and even this has been shown recently to have a far wider occurrence than had been previously thought (Travers, 1981; it may even occur in some ophichthid eels (McCosker, 1977 and M. Leiby pers. comm.).

Table 1 Teleostean outgroup taxa (supplementary to those listed in Travers 1981).

Species	Reg. No.	Preparation
Arapaima gigas	Unreg.	DS
Elops hawaiensis	1962.4.3: 1–25	A
Elops machnata	1962.8.28: 1–7	A
Halosaurus owenii	1890.6.16: 55	AP
Notacanthus bonapartei	1972.1.26: 33–39	MD
Notacanthus sexspinis	1873.12.13: 27	DS
Anguilla anguilla	1962.6.5: 2–4	MD
Etrumeus teres	1923.2.26: 73–78	A
Ostichthys parvidens	1974.5.25: 747–753	MD
Holocentrus rufus	1976.7.14: 79–81	MD
Zeus faber	1971.7.21: 86–90	MD
Hypoptychus dybowskii	1979.11.26: 1–3	MD
Macrotrema caligans	1860.3.19: 943 Type	AP
Macrotrema caligans	1908.7.13: 1	AP
Monopterus cuchia	Unreg.	DS
Synbranchus bengalensis	1860.3.19: 1477	MD
Synbranchus javanicus	1862.11.1: 138	MD
Synbranchus marmoratus	1981.1.15: 1117–1119	MD
Mugil cephalus	1913.7.10: 31–34	MD
Pholis gunnellus	1981.2.20: 446–479	MD
Pholidichthys leucotaenia	1974.3.14: 1	MD
Pholidichthys leucotaenia	USNM 206237	A
Pholidichthys leucotaenia	USNM Gift	AP
Scytalina cerdale	USNM 70801	AP
Notograptus guttatus	USNM Gift	A/A
Ptilichthys goodei	USNM 130266	AP
Stichaeus (Leptoblennius) mackayi	1896.7.23: 183	MD

Abbreviations

Anatomical

Aa	Anguloarticular
Add Mand	*Adductor mandibulae*
Asph	Autosphenotic
Bbl 1–3	Basibranchial 1–3
Bbl KC	Basibranchial I keel cartilaginous
Bh	Basihyal
Bh + Bbl	Basihyal fused with basibranchial I
BR	Branchiostegal rays
Bs	Basisphenoid
C	Cleithrum

Com	Coronomeckelian
DO	*Dilatator operculi*
Dsph	Dermosphenotic
Ect	Ectopterygoid
End	Endopterygoid
F	Frontal
Fa	Fimbria
FDL	Frontal descending lamina
FFac	Frontal facet
Fu	Fimbrule
Hb 2–3	Hyobranchial 2–3
Hb3 AP	Hyobranchial 3 anterior process
Hyo	Hyomandibula
Hyo Add	*Hyohyoidei adductores*
HyoMF	Hyomandibula metapterygoid flange
Hyo SP	Hyomandibula symplectic process
Iop	Interoperculum
LE	Lateral ethmoid
LE xsc	Lateral extrascapula
Lig	Ligament
LO	*Levator operculi*
MC	Meckel's cartilage
Met	Metapterygoid
MExsc	Medial extrascapula
MP	Maxillary process
Op	Operculum
P	Parasphenoid
Pal	Palatine
Palopt	Palatopterygoid
PalT	Palatine teeth
PAW	Parasphenoid ascending 'wing'
Pop	Preoperculum
Pr	Prootic
PrAP	Prootic anterior process
Pt	Pterosphenoid
Ptm	Posttemporal
PtmT	Posttemporal tubule
Q	Quadrate
Ra	Retroarticular
Sc	Supracleithrum
Sen Pap	Sensory papillae
Sep	Septum (ossified)
Sop	Suboperculum
Sph	Sphenotic
Sym	Symplectic
Uh	Urohyal
UhAP	Urohyal ascending process

Note on the figures: even stipple-dots indicate the presence of cartilage. The scale on all figures indicates 1 mm.

Table of study material

A/A	Double stained transparency (alizarin red and alcian blue)
A	Alizarin stained transparency
DS	Dry skeleton preparation
MD	Muscle dissection (cheek & opercular region)
AP	Alcohol preserved specimen not available for dissection or preparation
Unreg.	Unregistered specimen held at BM(NH)

Institutional

BM(NH)	British Museum (Natural History).
USNM	United States National Museum, Washington.

Mastacembeloid interrelationships

I. Character analyses

Osteology

NEUROCRANIUM

The neurocranium exhibits the general trends (mainly reductional) and particular features that are currently recognised as diagnostic for acanthopterygian fishes (see Zehren, 1979: 163–166 for a recent summary), although they are somewhat masked by the extreme precommissural attentuation of the skull. Of the eleven acanthopterygian neurocranial and circumorbital character states listed by Patterson (1964: 449) and Zehren (*op. cit.*) eight are readily recognisable in almost all mastacembeloids. A further derived feature found by Patterson (1975: 568) only in the Acanthopterygii is the pons moultoni, a loop of bone on the inner face of the sphenotic which surrounds the anterior semi-circular canal.

The medial face of the sphenotic in mastacembeloids houses the anterior semi-circular canal in such a structure and thus conforms to the condition in the Acanthopterygii. Surprisingly, Zehren (1979) did not mention the pons moultoni in his study of the Beryciformes.

Elongation of the supraethmoid and vomer in mastacembeloids contributes to the generally pointed snout in these fishes, although the lateral ethmoids are of more usual proportions (Travers, 1984). In other percomorphs with elongate syncrania, including such forms as the congrogadids, pholidichthyids, sphyraenids, acanthurids, luciocephalids and synbranchids, the ethmovomerine region is not always attenuated. In *Congrogadus subduceus* and *Pholidichthys leucotaenia* this region is of similar proportions to that found in most other percomorphs, any elongation being restricted to the postorbital neurocranial bones. In *Sphyraena obtusata, Acanthurus bahianus* and *Luciocephalus pulcher* the ethmovomerine region is particularly elongated, whilst the braincase proportions are similar to those in most percomorph fishes. This condition is produced in *Sphyraena* by elongation of the lateral ethmoids, whilst in *Luciocephalus* the prevomer and nasals are particularly lengthened (Liem, 1967). The anterior region of the parasphenoid is particularly long in *Acanthurus* and, combined with the long supraethmoid, it contributes to the elongate ethmovomerine region.

The vomer in synbranchids was described by Rosen & Greenwood (1976: 49) as a 'long, thin strut' elongated to a point below the pterosphenoids and basisphenoid. This is the only outgroup examined which has a vomerine shaft comparable in length to that in the mastacembeloids (e.g. compare the vomerine length in Rosen & Greenwood, 1976, figs. 57 & 59 with the vomer in other percomorphs). This may well be a synapomorphy of these taxa.

Although an elongate ethmovomerine region occurs in a variety of what appear to be phyletically distant percomorph fishes, the method by which elongation is achieved in the mastacembeloids (by extreme lengthening of the vomer and supraethmoid) is not found in any other group (apart from a similar elongation of the vomer in the synbranchids).

The sensory canal bearing bones of the ethmovomerine region (i.e. the nasal and 1st infraorbital) are also elongated, and the nasal has a particularly broad dorsal surface in mastacembeloids.

The 1st infraorbital is long and tapered in a variety of percomorphs, including the synbranchids, ammodytids and luciocephalids. However, the nasal in these taxa is barely broader than the sensory canal it carries.

The concomitant elongation in the mastacembeloids of the supraethmoid, vomer and 1st infraorbital bone, accompanied by a long nasal with a broad dorsal surface, results in a snout unlike that found in any of the other taxa examined. It is thus considered to be a synapomorphy for the group.

The mastacembeloid lateral ethmoid is not elongate although the 'ethmoids' (presumably including the lateral ethmoid) were included by Rosen & Greenwood (1976) in their list of 'greatly attentuated' mastacembeloid neurocranial elements. In fact the lateral ethmoids retain the general percomorph proportions, but are fused in the midline and have an overall tubular shape.

In percomorph fishes the lateral ethmoids are generally plate-like bones lying on either side of the supraethmoid and are separated from each other medially by the cartilaginous, posteroventral end (septal cartilage) of the supraethmoid.

Medial fusion of the lateral ethmoids in mastacembeloids, dorsal to the cartilaginous posterior end of the supraethmoid is an arrangement found also in blennioids, (e.g. *Notograptus guttatus*) and in gobioids (e.g. *Trypauchen wakae*). However, the tubular shape of the lateral ethmoids was not found in any other outgroup taxa.

The mastacembeloid pterosphenoids have wide lateral faces and are connected ventromedially (Travers, 1984: 51).

Among the outgroups examined (see Table 1) medial pterosphenoid connections were found only in the clupeid *Etrumeus,* some beryciforms (e.g. *Diretmus argenteus* and *Ostichthys trachypoma*; Zehren, 1979) and the anabantoids (e.g. *Belontia* and *Trichogaster leeri*; Liem, 1963).

In the anabantoids the pterosphenoids are not connected ventrally, but dorsally are linked by long wing-like processes, running transversely across the orbital cavity. In two beryciform families (Diretmidae and Holocentridae) Zehren (1979: 232) found the pterosphenoids to have their '... anterior lower edges meet in the midline closing off the optic fenestra' and, on the basis of outgroup comparisons concluded that this arrangement represented the apomorphic condition (see below).

In synbranchids the massive development of the pterosphenoids has been noted by Rosen & Greenwood (1976: 44) who found that, with the basisphenoid, these bones occupy '... somewhat less than half the total length of the neurocranium'. Although the pterosphenoid is large in synbranchids it does not contact its partner in the midline. Rosen & Greenwood (1976) also listed the bones involved in the neurocranial lengthening of mastacembeloids, when comparing them with synbranchids, but failed to mention the central role of the pterosphenoids.

The wide lateral face of the pterosphenoids and their medial union ventrally (resulting in the ventral half of the optic foramen being bounded by them) is a synapomorphic character of all the mastacembeloids (its absence in *Pillaia* and *Mastacembelus aviceps* is discussed on p. 110). In the beryciforms in which the pterosphenoids are connected in the midline (discussed above), these bones lack wide lateral faces and their medial connection is thought to be convergent with that in the mastacembeloids.

The basisphenoid is a characteristically small, compressed bone in mastacembeloids (Travers 1984: 53). This configuration appears to be directly associated with the median pterosphenoid connection, and represents a derived state of the large Y-shaped bone present in most teleostean lineages. It can be noted that in beryciforms and *Etrumeus,* taxa also with medially fused pterosphenoids, the basisphenoid retains its plesiomorphic condition.

A preorbital (or, more correctly, suborbital) spine that pierces the skin is a characteristic feature of almost all mastacembeloids (Travers, 1984). A preorbital spine is also present in halosauroids (*sensu* Greenwood, 1977) as described by McDowell (1973) and illustrated by Greenwood (*op. cit.* figs. 5, 7, 9, 10 & 14), and in some Ostariophysii (e.g. Cobitidae). However, in these fishes it is produced, respectively, from the maxilla or the lateral ethmoid, and is not homologous with the mastacembeloid preorbital spine. Here the spine is the posterior end of the large first infraorbital bone. In no other teleostean taxon is the first infraorbital developed in this way, and the presence of the spine is a further valuable synapomorphy of the mastacembeloids.

A long prootic, characterised by a distinct anterior process passing across the anterolateral face of the neurocranium and into the orbital cavity, is typical of most mastacembeloid taxa (Travers, 1984: 58).

This is contrary to the opinion expressed by Springer & Freihofer (1976: 37) that, 'In the highly specialised Mastacembelidae and Chaudhuriidae the parasphenoid also lacks an ascending process but either the prootic is entirely blocked by the pterosphenoid-pleurosphenoid bones from entering the postorbital margin or the pterosphenoid-pleurosphenoid bones are absent (D. E. Rosen, pers. comm.)'.

The plesiomorph condition of the teleostean prootic is one in which the anterolateral edge contributes to the posterior rim of the orbit. In a few, and diverse, taxa the anterior margin of the prootic is prevented from bordering the orbit by the ascending parasphenoid process, the pterosphenoid and/or the descending lamina of the frontal. This occurs particularly in taxa with elongate neurocrania, and is seen in some *Lates* species illustrated by Greenwood (1976: fig. 3).

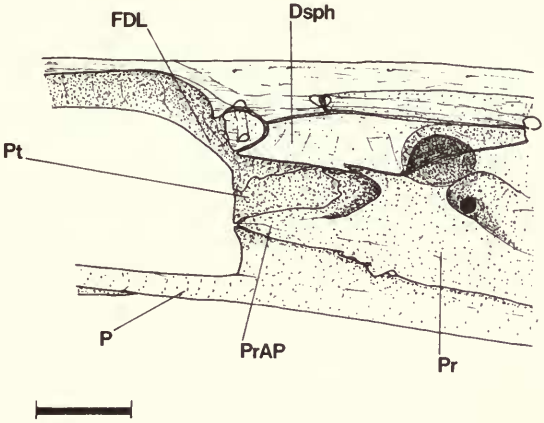

Fig. 2 *Congrogadus subduceus,* otic region of neurocranium; lateral view, left side.

A massive pterosphenoid and basisphenoid prevent the anterolateral extension of the prootic from entering the border of the small orbital cavity in the synbranchids (Rosen & Greenwood, 1976). In the Pholidichthyidae (Springer & Freihofer, 1976) the neurocranium is elongate and the prootic, lengthened anteriorly, has a wide lateral face, (Fig. 4a). The anterior region of the prootic in this taxon passess above the lateral face of the basisphenoid, and its anterior edge borders the posterior rim of the orbit. A very large prootic is also present in the congrogadids (e.g. *Congrogadus subduceus,* Fig. 2), and is distinguished by its long anterior region (between the ventral edge of the pterosphenoid and upper margin of the parasphenoid) which passes from the trigeminofacialis chamber to a point posterior to the rim of the orbit.

Thus, the large size of the prootic in mastacembeloids is not in itself exceptional. Rather, the exceptional feature is the anterior region of the prootic overlying the ventrolateral face of the pterosphenoid and being developed into a long anterior process extending into the orbital cavity. This constitutes a major synapomorphic feature of the mastacembeloid neurocranium.

The trigeminofacialis chamber lies in the prootic; its development has been discussed by Patterson (1964: 434–438). He concludes that the plesiomorphic condition for teleosts (as seen for example in *Elops*) was one in which the *truncus hyomandibularis,* the jugular vein and the orbital artery are separated by individual foramina in the pars jugularis. This condition differs from that in perciforms where the three foramina are confluent. The progressive reduction from four to two external openings in the pars jugularis among beryciform fishes has recently been demonstrated by Zehren (1979: 235) and lends support to Patterson's hypothesis (op. cit.) that '. . . during the evolution of teleosts there has been a simplification of the pars jugularis'.

A large trigeminal foramen (generally situated anterior to the lateral commissure) and a small facial foramen (generally medial to the lateral commissure) are the only foramina in the pars jugularis of mastacembeloids, which are apomorphic in this respect.

The mastacembeloid otic bulla is a small recess in the posteromedial face of the prootic, and completely houses the sacculus in most taxa. Only these fishes among the teleosts, have their saccular recess contained entirely within the prootic. In all others the recess is formed from the prootic, exoccipital and basioccipital. The relative contribution of these three bones does, however, vary from an almost equal contribution to one in which the greater part is derived from the prootic (e.g. congrogadids, tripterygiids of the genus *Paraclinus,* and *Channa obscura*).

This housing of the otolith bulla in the prootic only is a synapomorphic character of the mastacembeloids.

Precommissural elongation of the neurocranial bones in mastacembeloids involves that region of the autosphenotic lying anterodorsal to the lateral commissure (Travers, 1984: 69). This part of the sphenotic is produced into a wide anterolateral flange that generally extends across part of the lateral face of the pterosphenoid and descending frontal lamina, but does not enter the posterior border of the orbit. The postorbital process on the sphenotic, as a

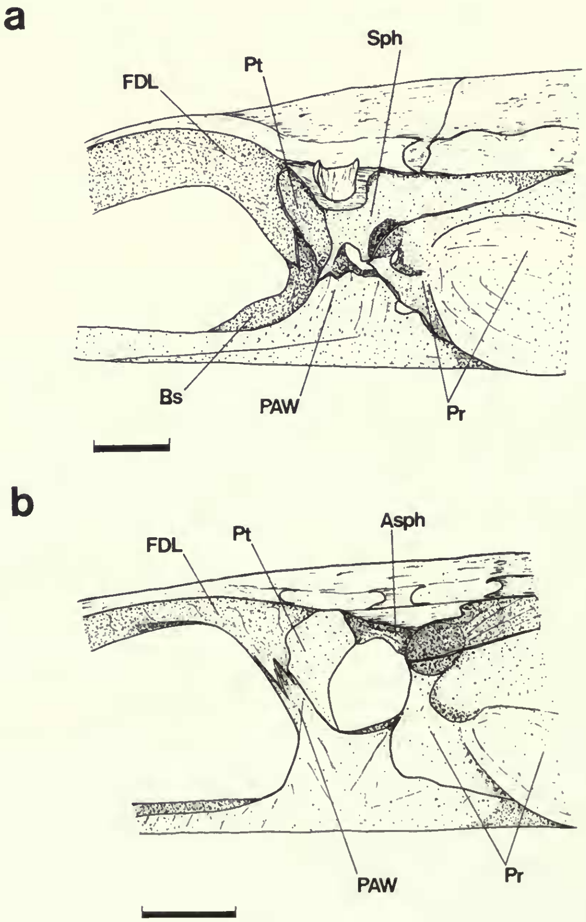

Fig. 3 Neurocranium of (a) *Ophidion rochei,* and (b) *Lycodes brevipes.* Left side of otic region, lateral aspect.

result of its anterolateral flange, has a posterior position relative to that of a similar process in other perciform fishes, for example the labroids (Rognes, 1973) and cichlids (Stiassny, 1981). This posterior position of the postorbital process indicates the extent to which the mastacembeloid sphenotic has expanded anteriorly.

In its plesiomorphic state the teleostean autosphenotic forms the posterodorsal corner of the orbit, a condition found in almost all major teleostean lineages, including many beryciform and perciform fishes.

Some development of the autosphenotic occurs in several phylogenetically distant acanthomorph lineages (e.g. *Ophidion rochei,* Fig. 3a; *Pholidichthys leucotaenia* and *Xiphistes mucosus,* Fig. 4a & b; *Ammodytes tobianus,* Fig. 4c), although in none is it developed to an extent comparable with that in the mastacembeloids, and in all the bone, unlike that in mastacembeloids, still forms the posterodorsal margin of the orbit. The ammodytoids, (e.g. *Ammodytes tobianus,* Fig. 4c) are the only other perciform group found to have a sphenotic with a wide anterolateral face. However, in these taxa the sphenotic forms the posterodorsal margin of the orbit and in this respect it retains the plesiomorph condition.

Thus, the condition of the wide anterolateral flange on the sphenotic in mastacembeloids which falls short of the postorbital margin, is a synapomorphy of the group.

The mastacembeloids lack a posttemporal fossa (Travers, 1984: 17). It is a common feature of lower teleosts and apart from having lost its bony roof, is widespread among higher euteleosts. In these fishes the posttemporal fossa generally lies lateral to the supratemporal fossa (Patterson, 1964: 449 & 1975: 392–5). Such fossae are typically found in the perciform neurocranium. The lack of a posttemporal fossa must, by virtue of the widescale presence of this fossa in teleosts, be a secondary loss and as such may be considered an apomorphic feature of these fishes. It is not, however, a feature restricted to these fishes. The fossa appears to have been lost independently in the following acanthomorph lineages: ophidioids (e.g. *Carapus acus*), synbranchoids (e.g. *Synbranchus marmoratus*), blennioids (e.g. *Notograptus guttatus*), trachinoids (e.g. *Trachinus vipera*) callionymoids (e.g. *Callionymus lyra*), acanthuroids (e.g. *Acanthurus bahrianus*) and channoids (e.g. *Channa obscura*).

A wide subtemporal recess in the posterolateral wall of the neurocranium, defined in part by the prootic, pterotic and exoccipital, is characteristic of all mastacembeloids (Travers, 1984) and is the site of origin for the levator musculature of the branchial arches. This recess, which is little more than a shallow lateral concavity, is not thought to be the homologue of the subtemporal fossa in lower teleosts (Forey, 1973; Patterson, 1975).

The occipital condyle in all mastacembeloid taxa is in the form of a tripartite, concave socket (Travers, 1984: 71) formed from equal contributions by the exoccipitals and the basioccipital. The hemispherical anterior face of the first centrum articulates in this socket.

A tripartite occipital condyle occurs in the majority of teleosts including the more basal assemblages (Forey, 1973: 12–19; Patterson, 1975: 318). Among these fishes the tripartite basi- and exoccipital facets are arranged in a variety of ways.

Rosen & Patterson (1969) recognised two general apomorphic conditions of the condyle in acanthomorph lineages. The paracanthopterygians they examined have the exoccipital facets displaced laterally, losing contact with the basioccipital facet, whereas, in the acanthopterygians they examined the exoccipital facets were displaced dorsally. Thus, the mastacembeloid arrangement in which the basi- and exoccipital facets are firmly joined into a single tripartite, concave socket is considered to represent an even more derived condition. However, this arrangement is not unique to mastacembeloids as the facets are also developed into a single concave socket in myctophids, polymixids and ammodytoids. In, for example, *Myctophum punctatum* (illustrated by Rosen & Patterson, 1969: fig. 61D) the anterior face of the first centrum is tightly fused with the occipital socket and cranial movement must be considerably restricted.

The tripartite occipital socket in *Polymixia japonica*, a species recently interpreted by Zehren (1979) as a basal percomorph, was also illustrated by Rosen & Patterson (1969: fig. 61E). In this taxon the anterior face of the first centrum has expanded into a convex condyle that fits into the occipital socket. This convexity of the first centrum may be the result of

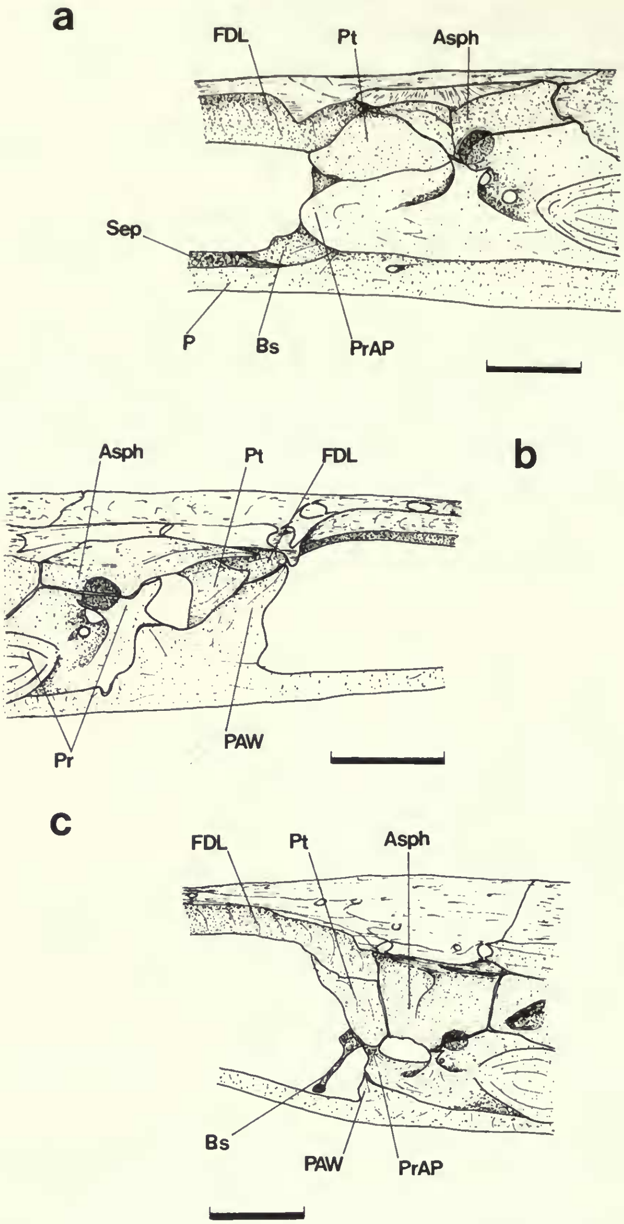

Fig. 4 Lateral view of neurocranial otic region in; (a) *Pholidichthys leucotaenia,* left side; (b) *Xiphistes mucosus,* right side; (c) *Ammodytes tobianus,* left side.

the osteoid cone (Patterson, 1975) having fused with it and the anterior part of the cone becomes rounded to fit into the occipital facet.

This apomorphic development of the anterior face of the first centrum has been taken a stage further in mastacembeloids. Here the anterior face is produced into a hemispherical condyle, that functionally forms a 'ball and socket' joint between the vertebral column and neurocranium. This is a synapomorphy of all mastacembeloids and is important evidence in support of the monophyletic origin of the group (see p. 108). In no other acanthopterygians, apart from the ammodytoids (Gosline, 1963), is there a 'ball and socket' joint between the vertebral column and neurocranium. Although the arrangement of the joint in ammodytoids is of a similarly derived type, in the absence of any further derived characters shared by these fishes it is thought that the resemblance is homoplastic.

The absence of a posttemporal bone was first noted by Regan (1912) in *Mastacembelus armatus* and is confirmed by all mastacembeloid taxa I have examined. In place of the posttemporal, 1–3 ossified tubules occur in most species.

Among teleosts, the only other groups lacking a posttemporal bone are the anguilloids, for example *Anguilla anguilla,* the notacanthids (McDowell, 1973: 137) and some siluroids (G. Howes, pers. comm.).

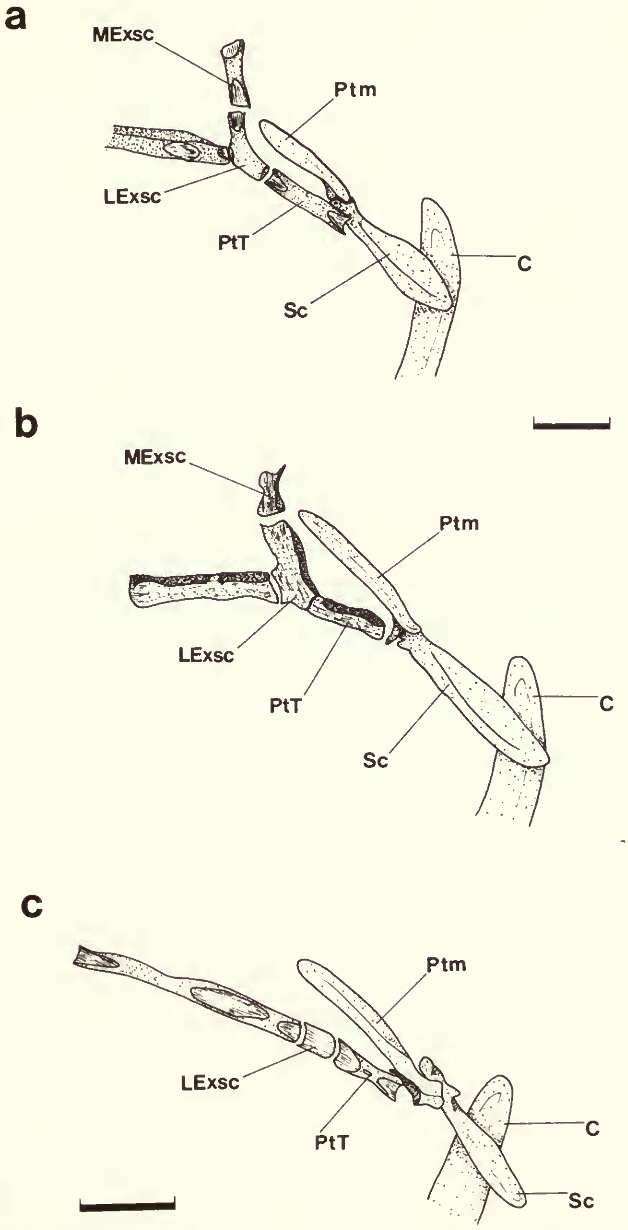

Fig. 5 Articulation of the left posttemporal bone to the pectoral girdle in: (a) *Zoarces viviparus;* (b) *Lycodes brevipes;* (c) *Dadyanos insignis.* Viewed obliquely from a dorsolateral position.

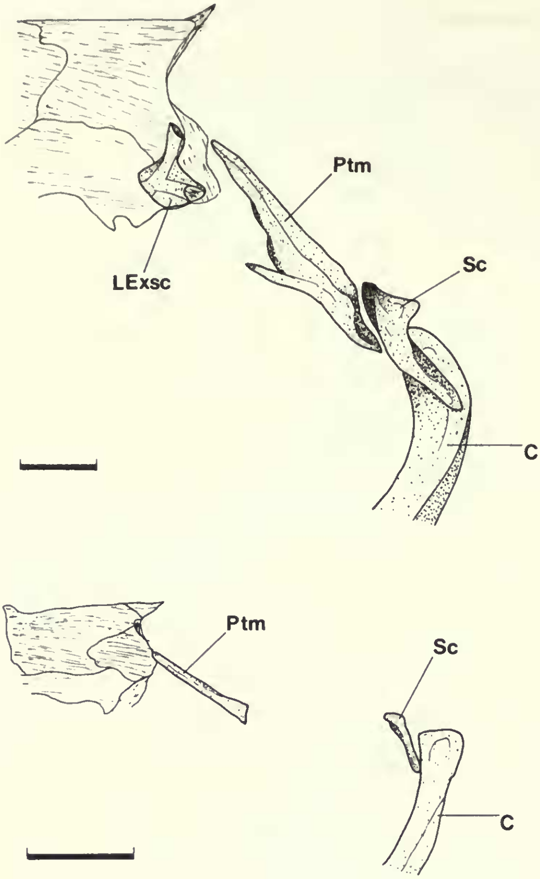

Fig. 6 Articulation of the left posttemporal bone in: (a) *Monopterus albus*; (b) *Synbranchus marmoratus*. Lateral view of the elements which are depicted *in situ*.

In the true eels the pectoral girdle lies posterior to the cranium, adjacent to the 7th or 8th abdominal vertebrae. The postcranial sensory canal in *Anguilla* passes through three small dermal tubules lying between the cranium and pectoral girdle.

Zoarcoids, for example *Zoarces viviparus*, *Lycodes brevipes* and *Dadyanos insignis* (Fig. 5), are also distinguished by their eel-like shape and posteriorly displaced pectoral girdle. This is connected to the neurocranium (epioccipital) by a narrow, blade-like posttemporal bone, through which the postcranial sensory canal does not run; instead it passess laterally, parallel to the posttemporal and is housed in two ossified dermal tubules.

From the condition in zoarcids it seems reasonable to conclude that the ossified postcranial tubules in mastacembeloids and some anguilloids are not necessarily remnants of the posttemporal.

The absence of a posttemporal distinguishes mastacembeloids from all other neoteleosts. Its loss, like that in some anguilloids (discussed above) and notacanthids (McDowell, 1973), is correlated with the posterior position of the pectoral girdle, (see Travers, 1984: 73).

The synbranchids also come into the category of eel-like neoteleostean fish with a reduced, posteriorly displaced pectoral girdle. A well-developed, forked, posttemporal connecting the basicranium to the pectoral girdle (generally adjacent to the 3rd & 4th abdominal vertebrae) occurs in *Monopterus albus* (Fig. 6a) and *Ophisternon* (Rosen & Greenwood, 1976: 63). On the other hand, in *Synbranchus* (e.g. *S. marmoratus*, Fig. 6b) the posttemporal is reduced to a narrow blade-like bone that tapers posteriorly from the basicranium (to which its anterior end is attached) and is not in contact with the pectoral girdle. The tendency in synbranchids towards reduction in size of the posttemporal is probably related to the position of the pectoral girdle. In its most derived condition (e.g. *S. marmoratus*) the posttemporal has lost its connection to the supracleithrum, an arrangment which, although unique to the synbranchids, could represent an early stage in the transformation of this bone to its condition in the mastacembeloids (i.e. complete loss). Unfortunately, suitable material of the most plesiomorph synbranchid—*Macrotrema elegans*—was not available for study.

Extrascapular bones are absent in all mastacembeloid taxa, (with the exception of *Mastacembelus brachyrhinus,* discussed below). The supratemporal arm of the cephalic sensory canal is completely enclosed in a transverse tube that passes across the parietal (Travers, 1984: 72). This canal surfaces at the medial edge of the parietal, and crosses the supraoccipital as an open channel, joining its partner in the midline.

The position of the supratemporal arm of the cephalic sensory canal in mastacembeloids may be the result of the lateral and medial extrascapulars (which generally house the canal) fusing along the posterodorsal surface of the parietal, or because true parietals have been replaced by extrascapulars (McDowell, 1973: 25). Alternatively, the extrascapulars may have been lost and the supratemporal sensory canal enclosed by the parietals during ontogeny.

In all mastacembeloids the parietal has a posterolateral flange (Travers, 1984: 72) that lies along the dorsal junction of the pterotic and epioccipital, and encloses the most lateral region of the supratemporal sensory canal. The expansion of the parietal in this region suggests that the extrascapulars may have fused with its posterodorsal surface, presumably in a manner similar to that described by Patterson (1977: 98) for the fusion between the median extrascapula and the supraoccipital in primitive clupeomorphs. Furthermore, in *Mastacembelus paucispinis* (Travers, 1984: fig 35a & c) a short, independent tubule, reminiscent of the posterior tubule-like region of the lateral extrascapula in other perciforms (e.g. *Perca fluviatilis*), is fused to the parietal between the pterotic and epioccipital. In my specimen of *Mastacembelus brachyrhinus* (uniquely among mastacembeloids) there is an independent lateral extrascapula on the dorsal surface of the parietal (albeit on the left side only, Travers, 1984: fig 37a & c).

The lateral and medial extrascapulae in higher euteleosts are short tubules which house the supratemporal arm of the cephalic sensory canal system as it traverses the dorsal surface of the neurocranium. Extrascapulae of this type are of widespread occurrence in the gadiform, batrachiodiform, cyprinodontiform, beryciform, scorpaeniform and perciform assemblages. In some of these the lateral and medial extrascapulae may be fused to the underlying parietal (dorsal surface), as seen for example, in the zoarcoids (e.g. *Zoarces viviparus* & *Lycodes muraena*) and some blennioids (e.g. *Malacoctenus delalandei, Haliophus guttatus, Acanthemblemaria maria* & *Congrogadus subduceus*). In all these examples the extrascapulae, although fused to the parietal, are clearly distinguishable, retaining their overall shape and size. However, in other blennioids including members of the Blenniidae (Springer, 1968) and Stichaeoidea (Makushok, 1958: his Stichaeoidae), extrascapulae are absent and the supratemporal sensory canal lies within the parietal. This arrangement of the supratemporal sensory canal, apart from the mastacembeloids, is found only in these blennioids among the teleosts examined.

In some percomorphs, however, the extrascapulae and the supratemporal arm of the sensory canal are both absent, for example in the gobioids and synbranchoids, as well as in *Chaudhuria* and *Pillaia* among the mastacembeloids (see below).

Thus, the total absence of discrete extrascapulae in mastacembeloids is a derived feature shared only with some blennioids. The lack of a supratemporal commissural sensory canal in *Chaudhuria* and *Pillaia,* taxa in which there appears to be a progressive reduction in the extent of the cephalic sensory canal system (see p. 113), may well be a further stage in such a trend (one convergent with that in the gobioids and synbranchoids).

JAWS

The upper jaw in mastacembeloids is non-protrusile and in this respect is rather exceptional among percomorphs; indeed, jaw protrusibility is a characteristic feature of most neoteleosts (Liem & Lauder, 1983).

Among percomorph fishes, relatively long premaxillary ascending processes and maxillary cranial condyles are absent only in the synbranchids and the mastacembeloids. The simple non-protrusile jaws in these taxa are similar to the plesiomorph teleostean condition seen in the osteoglossomorph, elopiform, clupeomorph and protacanthopterygian assemblages. Although the non-protrusile jaws in mastacembeloids and synbranchids appear to be of this type they have presumably been secondarily redeveloped from protrusile jaws (see Gosline, 1983: 324, discussed below p. 109 & 129).

The mastacembeloid dentary has a posteroventral extension (Travers, 1984: 80) which tapers posteriorly. This process extends from the rim of the posterior sensory canal opening and lies along the ventral edge of the anguloarticular. In representatives from nearly all major teleostean lineages (particularly neoteleosts) the posterior opening of the sensory canal in the dentary marks the posteroventral tip of this bone; e.g. in *Osteoglossum* (Kershaw, 1976); *Elops* (Forey, 1973); *Anguilla; Denticeps* (Greenwood, 1968); *Cyprinus; Salmo; Maurolicus; Chlorophthalmus; Myctophum; Percopsis; Gadus; Ophidion; Holocentrus* and *Serranus.*

In the numerous lower jaws taken from a wide selection of basal teleosts and illustrated by Nelson (1973), only that in *Arapaima gigas* (Nelson, 1973: fig. 2c & d) shows a process comparable with that in mastacembeloids, and must be considered a homoplasy. The dentary of *Arapaima gigas* illustrated in lateral view by Kershaw (1976: fig. 20, redrawn after Ridewood 1905) shows no posteroventral extension beyond the posterior opening of the sensory canal (the latter being clearly indicated); however, I have examined a skeletal preparation of *Arapaima gigas* and the long posteroventral process is clearly present.

Of the remaining lower jaws illustrated by Nelson there is a posteroventral extension of the dentary beyond the posterior sensory canal pore (albeit to a lesser extent than in the mastacembeloids) in some engraulids e.g. *Coilia mystus* and *Thrissina baelama* (Nelson, 1973: fig. 5 C, D & E, F).

Both these taxa are characterised by a long, pointed mandible, and the short posterior projection on the dentary may be regarded as homoplastic with that in mastacembeloids and *Arapaima.*

Among euteleosts, the synbranchids are the only group (apart from the mastacembeloids) in which there is a long posteroventral process on the dentary (illustrated by Rosen & Greenwood, 1976: fig. 60 & 61). This process extends beyond the posterior sensory canal opening along almost the entire ventral edge of the anguloarticular. Thus, it seems reasonable to conclude that the posterior extension of the dentary is a synapomorphy uniquely shared by mastacembeloids and synbranchids among euteleostean fishes.

The mastacembeloid mandible is also exceptional in the size and position of its coronomeckelian, a large bone (relative to the other mandibular elements) lying across the anterolateral face of the suspensorium.

A small coronomeckelian on the medial face of the anguloarticular is of common occurrence throughout the teleostomes (Starks, 1916), and this is taken to represent the plesiomorph condition both with regard to its size and position.

The coronomeckelian was shown by Starks (1916) to be the ossified anterior end of the A_3 tendon. In support of this view he cited the condition of these elements in *Spheroides annulatus* '... where the adductor tendon has obviously ossified for a short space leaving an interval of tendon between the ossified portion and the mandible'.

This interpretation can also be applied to the arrangement of the coronomeckelian in mastacembeloids, except that in these fishes the tendon has ossified dorsal to the mandible. Tendons may become ossified (forming a sesamoid bone) in regions where tendon movement produces opposing frictional forces, for example where the tendon runs across a bony prominence. The long A_3 tendon in mastacembeloids runs across such a prominence—the deep and somewhat bulbous anterolateral face of the ectopterygoid (Travers, 1984: fig. 5).

The development of the unusually large, dorsally situated coronomeckelian in mastacembeloids thus appears to be directly related to the shape of the ectopterygoid. The size and position of the coronomeckelian in *Chaudhuria* and *Pillaia* (discussed below), taxa which lack an ectopterygoid with a deep anterolateral face, is evidence in support of this view.

Although there is extensive variation in the size and shape of the coronomeckelian among teleosts, (see Fig. 7 a–g) in no other taxon is it comparable with that in mastacembeloids, for which it is taken to be a unique synapomorphy.

The dorsal edge of the anguloarticular is straight in most mastacembeloids (Travers, 1984: 82) and lacks a coronoid process in all taxa except *Macrognathus,* where the coronoid elevation is low and broad based (see Travers, 1984: 80).

The anguloarticular lacks a coronoid process in about half the synbranchid species recognised by Rosen & Greenwood (1976: 45), and this characteristic was considered to be of some phylogenetic interest by these authors. They were of the opinion that, 'Such coronoid prominences on the articular of teleosts are common, although in many unrelated fishes with elongate crania and jaws the process is absent'. The absence of a coronoid process on the anguloarticular in synbranchoids was thought by Rosen & Greenwood (1976) to be a plesiomorph feature of the taxon, and the processes present in *Monopterus albus* and *Ophisternon* species were thought to be independently gained autapomorphies.

A coronoid process is absent on the anguloarticular in a variety of teleosts including the anguilloids (e.g. *Anguilla anguilla*), some percoids (e.g. *Scarus croicensis*), blennioids (e.g. *Notograptus guttatus* and *Pholidichthys leucotaenia* [very low projection]), many gobioids (e.g. *Gobius niger; Aphia minuta; Amblyopus brousonetti* and *Crystallogobius linearis*), and notothenioids (e.g. *Notothenia sema* [very low projection]). These observations support the view held by Rosen & Greenwood (op. cit.) that many unrelated fishes lack a coronoid process and that its absence in percomorph lineages is plesiomorphic.

PTERYGO–PALATINE ARCH

Regan (1912) found that in mastacembeloids the '... pterygoid is movably articulated with the lateral ethmoids external to the palatine', and noted that they are 'very perculiar' in these fishes.

The ectopterygoids are large bones characterised by a deep anterolateral face and their direct connection to the lateral ethmoids (Travers, 1984: 83). This direct articulation of the large ectopterygoid (functionally replacing the palatine which lacks articulatory facets; see below) is the sole means by which the anterior end of the suspensorium is joined to the neurocranium in most mastacembeloid taxa. The articulation of the suspensorium to the neurocranium in almost all other euteleosts involves the palatine. Among lower teleosts, the palatine also plays a central role in suspensorial articulation with the neurocranium, although this does not necessarily exclude the ectopterygoid from having an articulatory function in some taxa, as for example in the osteoglossoids. In *Osteoglossum* there is only a single element in place of the ectopterygoid and palatine, which are, in the opinion of Kershaw (1976: 192), 'indistinguishably connected'. The anterior end of the 'ecto-palatine' bone is ligamentously connected to the lateral ethmoid in *Osteoglossum.*

The ectopterygoid is enlarged anteriorly in some halosauroids (Greenwood, 1977); however, in none does it articulate directly with the ethmoid region. Anguilloids too generally have an elongated suspensorium and in *Anguilla anguilla* (Fig. 8) its anterior articulation is effected by a long, narrow bone which extends to the ethmoid region and may incorporate the palatine (the palatopterygoid of Matsui & Takai, 1959) because an ossified autopalatine was not observed in *Anguilla*. This bone was considered by Norman (1926) to be an endopterygoid.

More recently, Leiby (1979 & 1981) has found that in several ophichthid anguilloids the endopterygoid and metapterygoid form a single compound bone which fuses during ontogeny with the anterior edge of the hyomandibula. He identifies the long narrow bone connecting the suspensorium and neurocranium as an ectopterygoid in these fishes (Leiby, 1979: fig. 2F & 1981: fig. 12A).

The suspensorium in *Anguilla* has, superficially, a remarkably similar apearance to that in several of the more highly derived mastacembeloids, particularly *Chaudhuria* and *Pillaia*

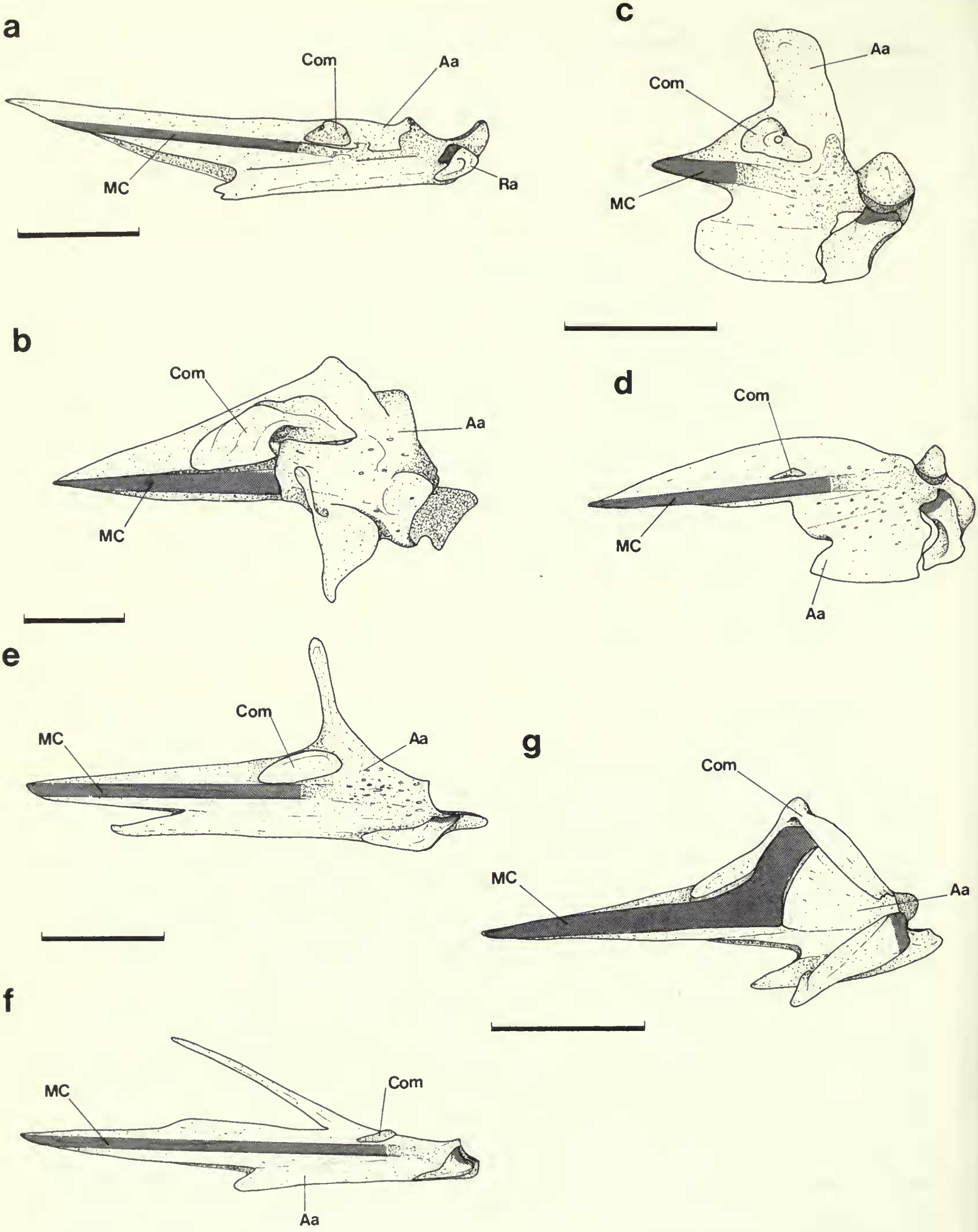

Fig. 7 Medial view of the right coronomeckelian in: (a) *Notograptus guttatus*; (b) *Rhyacichthys aspro*; (c) *Trichogaster leeri*; (d) *Sandelia capensis*; (e) *Luciocephalus pulcher*; (f) *Hypoptychus dybowskii*; (g) *Callionymus lyra.*

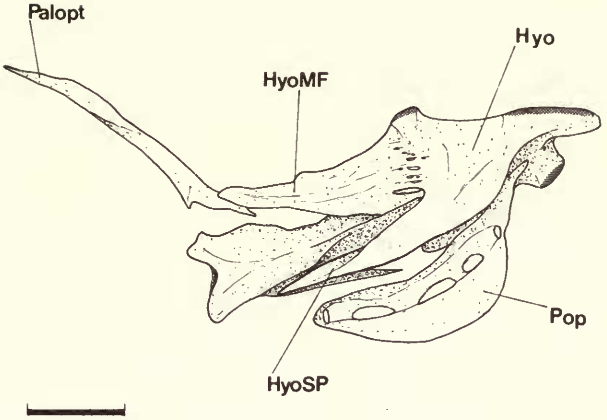

Fig. 8 *Anguilla anguilla,* left hyopterygoid arch and preoperculum in lateral view.

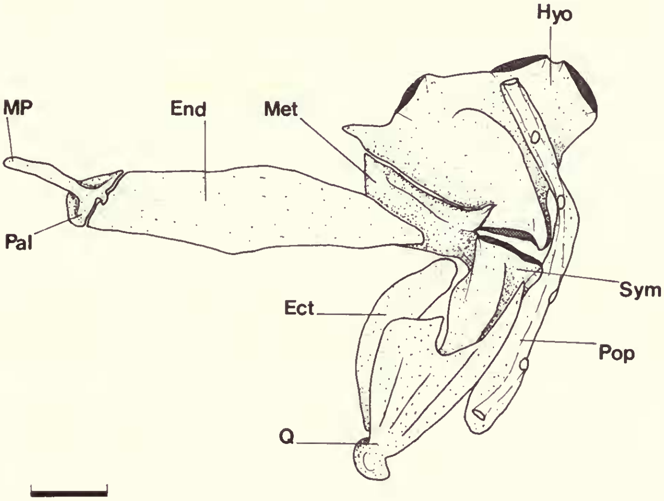

Fig. 9 *Congrogadus subduceus,* left hyopalatine arch and preoperculum in lateral view.

(e.g. compare Travers, 1984: figs. 17 & 25 with Fig. 8). However, its anterior articulation in *Anguilla* is effected by what is apparently the ectopterygoid (which may have fused with the palatine) articulating with the ethmoid region and maxilla, whereas, in *Chaudhuria* and *Pillaia* the ectopterygoid, which is also attenuated (and possibly fused with the palatine), articulates with the lateral face of the vomerine shaft (see Travers, 1984: 83).

The endopterygoid is enlarged, functionally replacing the ectopterygoid, in the congrogadids. In *Congrogadus subduceus* and *Haliophus guttatus* (Fig. 9) the anterior end of the bone is connected to the palatine which articulates the suspensorium with the neurocranium. The ectopterygoid in these species is a short, narrow bone connected to the anterior edge of the quadrate, and lacks an anterior point of articulation with the skull.

In synbranchids there is a large ectopterygoid which Rosen & Greenwood (1976: 44–48) imply is associated with the absence of the endopterygoid and with the massive development of the basisphenoid. They term this trend one of the 'special' attributes of all synbranchids. In *Synbranchus marmoratus* (Fig. 10) the ectopterygoid is connected posteriorly (by its anterodorsal, but subdistal process) to a basisphenoid projection, and also has a more usual distal articulation with the palatine. This additional abutment has developed between the ectopterygoid and frontal in *Ophisternon aenigmaticum* (Gosline, 1983: fig. 3B). The degree

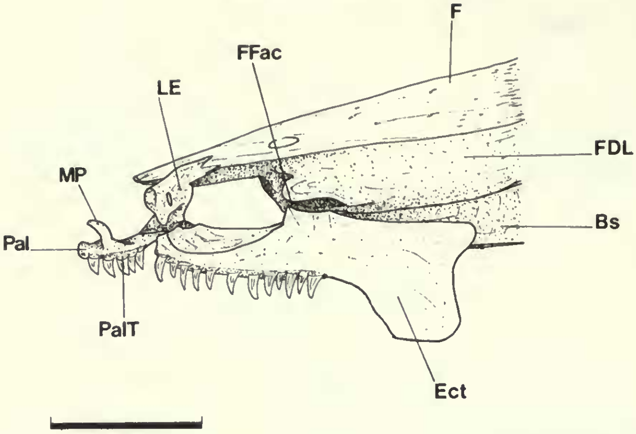

Fig 10 *Synbranchus marmoratus*, left palatopterygoid articulation to the neurocranium, lateral aspect.

of enlargement of the ectopterygoid is particularly great in *Monopterus albus* (compare Rosen & Greenwood, 1976: figs. 59 & 61).

The palatine in *Monopterus* lies further anteriorly than that in *Synbranchus* (e.g. compare Rosen & Greenwood, 1976: figs. 58 & 59) and its articulatory function (between suspensorium and lateral ethmoid) is taken over by the ectopterygoid in both species.

The increase in the size of the ectopterygoid in synbranchids (p. 110) must be an apomorphic feature because it culminates in the anterior displacement of the palatine (associated with a reduction in the size of its maxillary process and its close adherence to the vomerine shaft) and, consequently, the establishment of a direct articulation between the ectopterygoid and lateral ethmoid in some taxa (e.g. *Monopterus*).

Apart from these highly modified synbranchids, a direct articulation between the ectopterygoid and the lateral ethmoid is an otherwise distinctive synapormorphy found only in the majority of mastacembeloids.

A long, thin palatine sutured along the posterolateral face of the vomerine shaft, and lacking articulatory facets, is a characteristic feature of most mastacembeloid taxa.

In those euteleosts with a distinct palatine this bone generally has moveable joints with the neurocranium and the upper jaw, *viz.*, with the lateral ethmoid, usually involving a medial palatine facet, and anteriorly with the maxilla (cranial condyle) usually involving a short, often curved, maxillary process developed from the palatine. Although the palatine in higher euteleosts is variable in shape and dentition it was found to possess these articulatory functions in most lineages except the mastacembeloids and synbranchids.

The mastacembeloid palatine is a straight bone that is sutured to the lateral face of the vomer/parasphenoid junction below the lateral ethmoid to which it may be connected by a weak ascending spur (Travers, 1984: 84). It lacks any moveable articulation and does not have a maxillary process. Posteriorly, the palatine extends below the orbit, is dorsoventrally flattened, and supports the anterior fibres of the *adductor arcus palatini* muscle in this region. This highly derived palatine is typical of all mastacembeloids and is presumably associated with the lack of a protrusile upper jaw.

The reductional trend in the synbranchid palatine is probably also associated with the loss of protrusibility of the upper jaw.

In the more highly derived synbranchids (e.g. *Monopterus*) both the close adherence of the palatine to the vomerine shaft, and the lack of its connection to the lateral ethmoid are derived features (synapomorphies) shared with the mastacembeloids but with no other higher euteleosteans. Development of the mastacembeloid palatine appears to be at a more derived stage (i.e. no maxillary process or connection to the ectopterygoid) than is the synbranchid palatine. This arrangement of the palatine in mastacembeloids and synbranchids is closely associated with the development of the ectopterygoid in these taxa and, in combination, these characters provide important evidence in support of an hypothesis of shared common ancestry for the two groups, evidence consistent with the indications provided by the dentary (see p. 98) and posttemporal (p. 96) bones.

BRANCHIAL ARCHES

In most mastacembeloids a small, round, toothplate is fused to the dorsal surface of hypobranchial 3 (see also Maheshwari, 1965: fig. 6). Apart from these fishes a fused toothplate features (see p. 103), it could be a reliable synapomorphy for uniting these groups. Its (e.g. *Nandus* & *Badus*) and channids (e.g. *Channa*). The possible means by which this fused toothplate has developed in *Nandus, Badus* and *Channa,* and its value as an indicator of phyletic relationships were discussed by Nelson (1969: 496–7).

A fused toothplate on hypobranchial 3 is absent in *Mastacembelus mastacembelus, Pillaia* and in an assemblage of African species (Travers, 1984: 94).

In those species in which the toothplate is present, it is not always opposed by toothplates on epibranchial 1. Toothplates on that element occur only in the larger predaceous species (e.g. *Mastacembelus cunningtoni;* Travers, 1984: fig. 64). Although a fused toothplate on hypobranchial 3 is a synapomorphy uniting most mastacembeloids, its mosaic distribution within the group and its occurrence in several phylogenetically distantly related taxa make it a character of limited taxonomic value when considered in isolation.

A pair of processes descending from the posterolateral corners of basibranchial 2 are present in most mastacembeloids. The ventral tips of these processes are curved anteriorly and connect by converging ligaments to the posteroventral margin of basibranchial 1 (Travers, 1984: 92). Processes on basibranchial 2 have not been found in any outgroup taxa, their presence is treated as a synapomorphic character of the mastacembeloids, and further evidence in support of their monophyletic origin.

DORSAL FIN SPINES

The development of a series of spinous rays in the dorsal fin is a feature common to most acanthopterygian fishes. The number of dorsal spines may vary from a short row to a long series along the entire length of the dorsal surface in some fishes, e.g. the 'prickleback', *Stichaeus hexagrammus.* The spinous dorsal rays, regardless of their number, are generally interconnected by a thin membrane, however, this is absent in mastacembeloids.

Isolated dorsal spines appear also in several notacanthid halosauroids. However, the spinous rays in these fishes have been shown by McDowell (1973: 143) to form '... part of a (single dorsal) connected fin ... that is low and so heavily sheathed by scaly skin that only the separate tips of the spines are visible without dissection'. Furthermore, all these fishes lack a series of soft-rays posterior to the spinous part of the dorsal fin.

Thus a dorsal fin composed of isolated short, stout spines anterior to a long series of soft rays must be a synapomorphy of the mastacembeloids as it is unique to the group.

Myology

CEPHALIC MUSCLES

A number of myological features common to several mastacembeloid taxa were found to be unique to the group.

The mastacembeloid *levator operculi* originates from the pterotic and inserts on the dorsolateral face of the operculum in all taxa examined (Travers, 1984: 119). The insertion of a *levator operculi* was described by Winterbottom (1974: 238) as the dorsal or dorsomedial face of the operculum. This is the condition in the majority of teleosts I have examined, and must be considered the plesiomorphic condition in neoteleosteans. A lateral insertion of fibres of the *levator operculi,* apart from in the mastacembeloids, was only found in species of the phylogenetically distantly related anguilloids (e.g. *Anguilla anguilla*), synbranchoids

(Liem, 1980*a*: 83) and blennioids (e.g. *Notograptus guttatus*). The lateral insertion of *levator* fibres in all mastacembeloid and synbranchoid taxa suggests that, together with several other features (see p. 103), it could be a reliable synapomorphy for uniting these groups. Its occurrence in anguilloids and some blennioids in the absence of any further derived characters shared by these taxa and the mastacembeloids and synbranchoids, is interpreted as a convergence.

A small independent muscle lies between the posterior edge of the preoperculum and anterolateral face of the operculum (ventral to the opercular lateral ridge) in all mastacembeloids (Travers, 1984: fig. 79a), and is termed the '*musculus intraoperculi*' (Travers, 1984: 120) because of its position within the opercular series. Winterbottom (1974) describes no

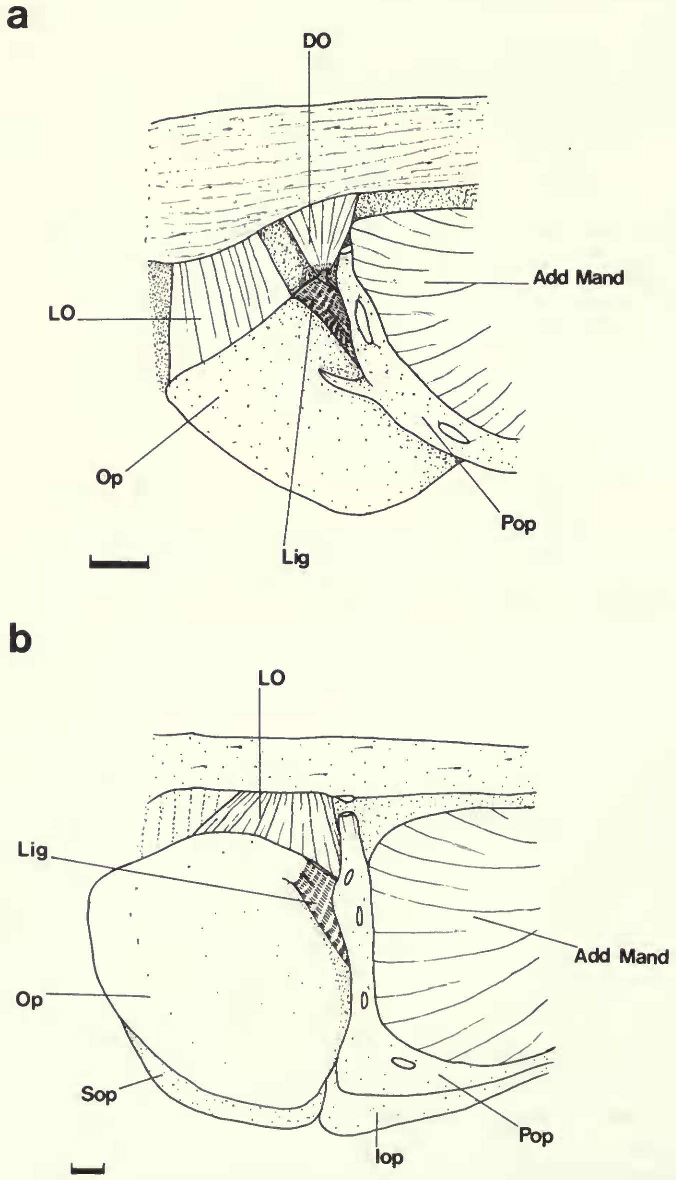

Fig. 11 Ligamentous connection between the preoperculum and operculum in: (a) *Cottus gobio*; (b) *Channa obscura*. Lateral view, right side.

muscle in this position in any teleost he examined; its absence is confirmed by all outgroup taxa I have examined. Its unique occurrence in the mastacembeloids is a valuable synapomorphy for the group.

A ligament between the posterior edge of the preoperculum and the anterolateral face of the operculum occurs in a number of phylogenetically diverse acanthomorph taxa. These include the cottoids (e.g. *Agonus cataphractus*, with a weak ligament between the preoperculum and operculum and *Cottus gobio* with a broad strong ligament; Fig. 11a), the gobioid *Amblyopus broussonetti* (in which a broad, weak collagenous band lies between the preoperculum and operculum) and the channoids (e.g. *Channa obscura*, with a strong opaque ligament; Fig. 11b).

An origin of the *adductor hyomandibulae* from the posteroventral surface of the parasphenoid is not recorded by Winterbottom (1974: 240), but this condition is typical of all mastacembeloids (Travers, 1984: 125). Also, a musculous insertion of this muscle partly on the medial face of the symplectic seems to be a general feature of all mastacembeloids and one not found in other groups (Winterbottom, 1974 gives the muscle's insertion site as the 'posterodorsomedial face of the hyomandibular').

The arrangement of these features of the *adductor hyomandibulae* were not always readily discernible in the outgroup taxa I examined they, therefore, remain doubtful additional synapomorphies of the group.

The dorsal expansion of fibres of the *hyohyoidei adductores* above the upper branchiostegal rays (medial to the suboperculum and operculum) and their insertion on the cleithrum, supracleithrum and posttemporal tubules in mastacembeloids (Travers, 1984: 128) is an unparalleled apomorphic development of this muscle. The general condition of the *hyohyoidei adductores* in teleosts is as a medial sheet of fibres extending only between the distal portions of the branchiostegal rays. Winterbottom (1974) noted that the fibres may continue dorsally above the posterodorsal ray to attach to the medial faces of some of the opercular bones, but in no teleost did he find the dorsal expansion continuing above the operculum and across the lateral face of the body muscles. I have examined the *hyohyoidei* in representatives of each major teleostean lineage, particularly those in which the opercular opening is restricted.

The anguilloids, e.g. *Anguilla anguilla,* have a very restricted opercular opening effected in part by the filiform branchiostegal rays which curve up around the posterodorsal corner of the operculum; see McAllister (1968: 79). Fibres of the *hyohyoidei adductores* pass across the medial face of these long branchiostegal rays, but do not extend further dorsally or insert on the lateral face of the body. McAllister (*op. cit.*) found a close resemblance between the anguilloid branchiostegal arrangement and that in the myctophoids. Here the *hyohyoidei adductores* are of general teleostean proportions.

The ophidioids (e.g. *Carapus acus*), zoarcoids (e.g. *Zoarces viviparas*) some blennioids (e.g. *Pholis gunnellus*), callionymoids (e.g. *Callionymus lyra*) and the tetraodontoids (e.g. *Diodon*) are all acanthomorph lineages with some restriction of the opercular opening. In none, however, do the *hyohyoidei* expand across the lateral wall of the body, although in some tetraodontoids they may expand medially and contact their partners in the midline (Winterbottom, 1974).

The synbranchids (particularly members of the Synbranchinae; Rosen & Greenwood, 1976) have a very restricted opercular opening. The 4–6 branchiostegal rays may have their distal halves poorly ossified in a number of synbranchids (Rosen & Greenwood, 1976), and although the family is characterised by small opercular bones, the branchiostegal apparatus and its musculature are hypertrophied (Liem, 1980*a* & *b*; fig. 14 in each). The fibres of the *hyohyoidei adductores* lie laterally across the branchiostegal rays in *Synbranchus marmoratus* (Fig. 12) and expand dorsally (the fibres running vertically, medial to the operculum) to a point above the operculum and over the lateral wall of the body (see also Liem, *op cit.*). The anterior fibres of the *hyohyoidei* in these synbranchids are also expanded dorsally (medial to the preoperculum), and form a distinct muscle slip, whose dorsolateral fibres insert on the medial face of the preoperculum and the anteromedial face of the

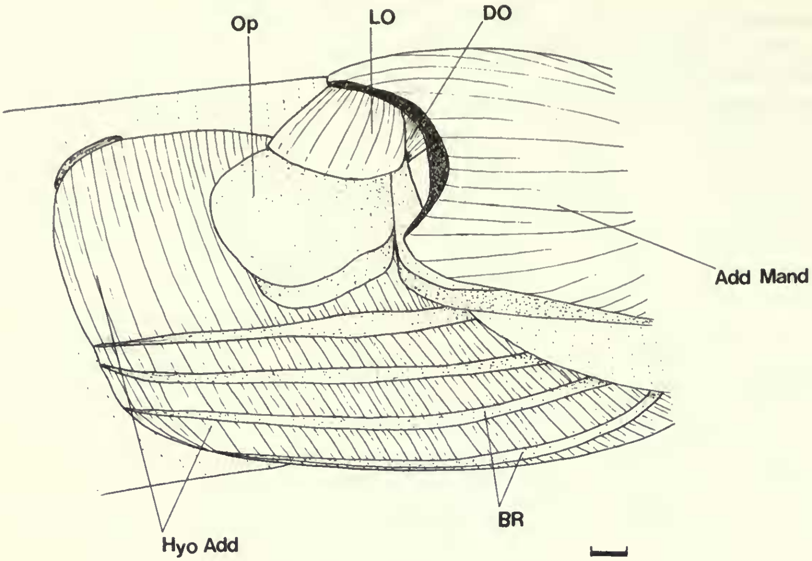

Fig. 12 *Synbranchus marmoratus,* right *hyohyoidei adductores* muscle, in lateral view after removal of the skin and part of the superficial *adductor mandibulae* musculature (to expose the *levator* and *dilatator operculi* muscles).

operculum, crossing the lateral border between these bones. Liem, however, makes no reference to this distinct anterodorsal slip of muscle fibres in either *Synbranchus* or *Monopterus.* Unfortunately, material of *Macrotrema caligans,* the most plesiomorphic synbranchid (Rosen & Greenwood, 1976) which has a comparatively unrestricted operculum (relative to other synbranchids), was unavailable for dissection.

The *hyohyoidei adductores* were considered by Liem (1980*a* & *b*; his *hyohyoideus*) as probably '... the most specialized muscle in synbranchiforms' as it is large and thick, occupies the entire ventrolateral surface of the branchial region and has its dorsal region (*hyohyoideus superior*) developed to such an extent that the upper fibres pass between the 1st and 2nd branchiostegals to the operculum (inner aspect) and pectoral girdle (supracleithrum & cleithrum). This arrangement of the *hyohyoidei adductores* closely resembles that in mastacembeloids (see Travers, 1984: fig. 79a and compare with fig. 14 in Liem, 1980*a* & *b*) and is an important synapomorphy of these taxa and further evidence in support of their hypothesised sister group relationship (see p. 104). This evidence is corroborated by the anterior slip of muscle fibres on the *hyohyoidei* in synbranchids, since a lateral migration of these fibres between the posterior edge of the preoperculum and anterolateral face of the operculum would result in a muscle having the same position and skeletal relationships as the '*intraoperculi*' muscle of mastacembeloids.

The presence of this muscle slip in synbranchids suggests that the mastacembeloid '*intraoperculi*' muscle could have developed from the *hyohyoidei adductores.* The innervation of the '*intraoperculi*' may well give a useful clue to its origin. If developed from the *hyohyoidei* the mastacembeloid arrangement should be considered as phylogenetically more advanced than that of the synbranchids.

The anterior tendinous insertion of the *obliquus superioris* on the posteroventral edge of the exoccipital is a feature of all mastacembeloids (Travers, 1984: 128). Anteriorly, its fibres do not fuse with the ventral surface of the epaxialis musculature. The anterior insertion of the obliquus tendon is described by Winterbottom (1974: 296) as being on to the posterolateral otic region of the skull, often extending forward beneath the orbit along the parasphenoid and even reaching the vomer. An exoccipital insertion for the *obliquus superioris*

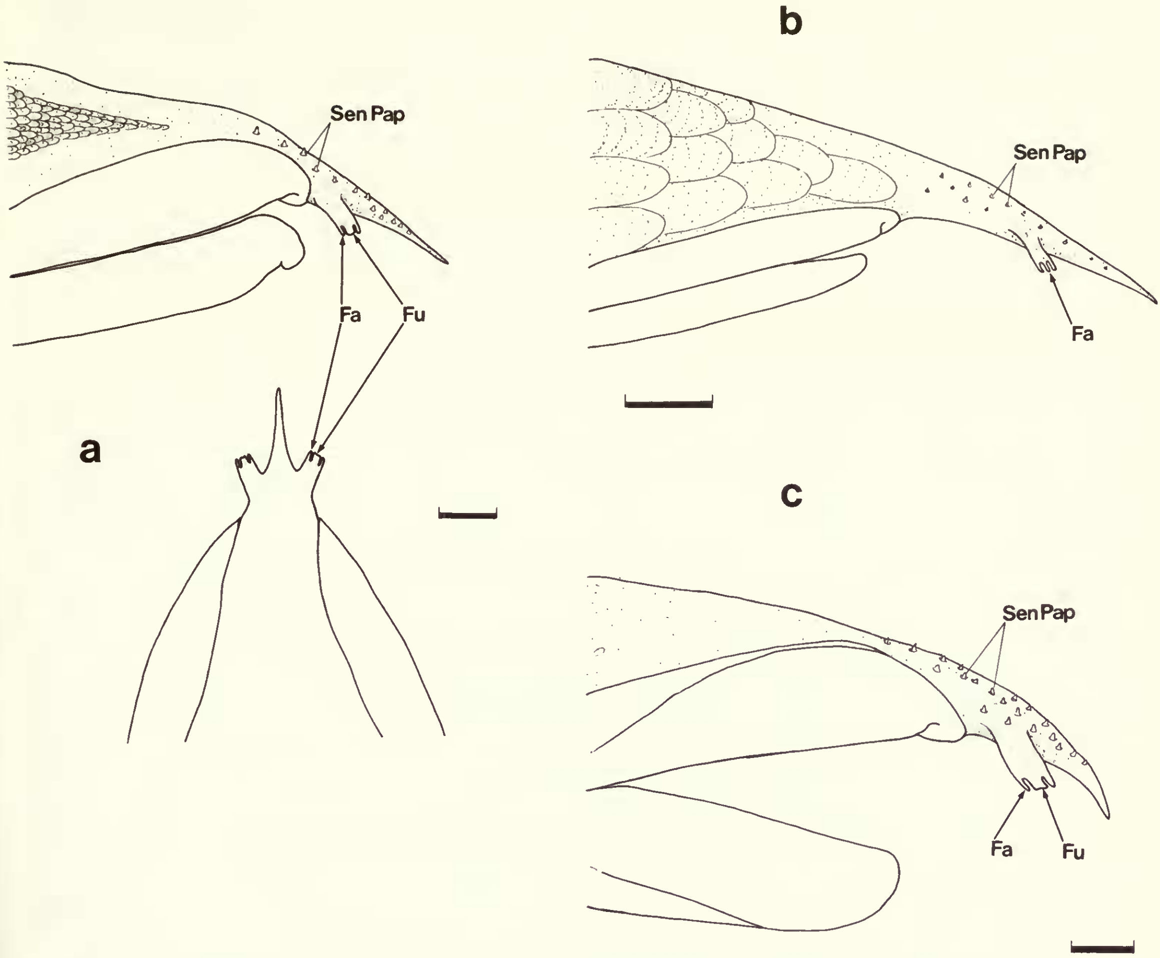

Fig. 13 Lateral view of the rostral appendage including the fimbriae and fimbrules surrounding the rim of the anterior nostril in: (a) *Mastacembelus moorii* (and dorsal view); (b) *Mastacembelus pancalus*; (c) *Mastacembelus mastacembelus*.

was not found in any other taxon than the mastacembeloids, and can be considered as a synapomorphy for the group.

The condition of Baudelot's ligament in mastacembeloids (Travers, 1984: 122 & 128) is uncharacteristic of its arrangement in higher enteleosts as described by Winterbottom (1974), who made no reference to it ever becoming bifurcated. Although dissection was not always possible, in those outgroups in which Baudelot's ligament was revealed on no occasion was it found to have a forked posterior end. The position of this ligament in mastacembeloids, with its dual connection to the pectoral girdle, appears to be a unique feature that may be tentatively interpreted as derived in comparison to the general arrangement and synapomorphous for the group.

Two other mastacembeloid features not found in any outgroup also warrant description: A rostral appendage, composed of two long, tubular extensions from the olfactory sacs lying on either side of a central rostral tentacle, is found in all but one mastacembeloid. This structure (described by Sufi, 1956 and Gosline, 1968: 61 & 1983: 323) is developed to a varying extent, from the very short appendage in *Mastacembelus moorii* (Fig. 13) to the large trunk-like appendage in *Macrognathus aculeatus* (Travers, 1984: fig. 45c & 46c).

A tubular anterior nostril is found in a number of phyletically diverse teleosts, from the anguilloids (e.g. *Anguilla anguilla*) to the channoids (e.g. *Channa obscura*). However, in none apart from the mastacembeloids, is the anterior tubular extension of the olfactory sac associated with a central rostral tentacle. Such a rostral appendage is an important synapomorphic character of the mastacembeloids, and is present in all taxa except *Chaudhuria*. The absence of a rostral appendage in this highly reduced and rather aberrant mastacembeloid is discussed below.

The presence, as in mastacembeloids, of a massive *nervus olfactorius* running through the centre of the lateral ethmoid (see Poll, 1973: plates IV & V), has not been found in any other teleostean lineage. This arrangement of the *nervous olfactorius,* particularly its massive size, is considered as synapomorphous for the mastacembeloids.

II. Defining characters of the Mastacembeloidei

The foregoing comparison of mastacembeloid anatomical characters with those in other teleostean fishes revealed 18 synapomorphies (represented by the 1st node in the cladogram Fig. 19) that may be used to support an hypothesis for the monophyletic origin of the Mastacembeloidei. In summary, these characters are:

1. Concomitant elongation of the supraethmoid, vomer and 1st infraorbital bone, accompanied by a long nasal with a broad dorsal surface.
2. Tubular lateral ethmoids.
3. Wide anterolateral face of the pterosphenoid and its ventro-medial connection to its opposite number; a feature associated with a very compressed basisphenoid.
4. Preorbital spine formed by the enlarged 1st infraorbital bone.
5. Long anterior process on the prootic that passes across the anterolateral (precommissural) wall of the braincase and into the orbital cavity.
6. Wide anterolateral flange on the sphenotic associated with the posterior position of the postorbital process.
7. Small saccular bulla housed entirely within the prootic.
8. Large coronomeckelian, lying dorsally across the anterolateral face of the suspensorium.
9. Ventral processes on basibranchial 2.
10. Long dorsal (and anal) fin composed of isolated short, stout spines unconnected by membrane, anterior to a long series of soft branched rays.
11. The presence of a '*musculus intraoperculi*'.
12. Anterior, tendinous insertion of the *obliquus superioris* muscle on the posteroventral edge of the exoccipital.
13. Baudelot's ligament forked posteriorly, connected to the supracleithrum and cleithrum, lying between the *obliquus superioris* and expaxialis muscles.
14. Anterior nasal openings at the end of long tubular epidermal extensions of the olfactory sac lying on either side of a central rostral tentacle.
15. Massive *nervus olfactorius* connecting the telencephalon with the olfactory organ.
16. Loss of lateral and medial extrascapular bones, associated with the incorporation of the supratemporal branch of the cephalic sensory canal system into the parietal.
17. Round toothplate fused to the dorsal surface of hypobranchial 3.
18. Development of the tripartite occipital facet into a concave socket, the anterior face of the first centrum into a hemispherical condyle and their articulation as a 'ball and socket' joint.

Of these synapomorphies, 1 to 15 do not appear in any other teleostean lineage examined as part of this study. These 15 features are unique to the mastacembeloids and conclusive evidence in support of the group's monophyletic origin. Of the remaining characters, 17 is shared mosaically, with a few and distantly related taxa; 16 is shared with some blennioids, and 18 is shared with the ammodytoids. Characters 16 to 18 are considered to be convergent in these taxa which do not share any other apomorphic features with the mastacembeloids.

On the basis of these synapomorphies the species at present recognised as constituting the mastacembeloids, i.e. *Chaudhuria caudata, Pillaia indica* (and *Garo khajuriai*: a second pillaiid species given separate generic status on the basis of slight superficial and morphometric dissimilarities, in a paper that became available only after this work had gone to press; Yazdani & Talwar, 1981), *Macrognathus siamensis, Macrognathus aral, Macrognathus aculeatus*, 15 Oriental *Mastacembalus* species (after Sufi, 1956) and about 46 African *Mastacembelus* species (see Travers, 1984: table 1) are all placed in a single taxon whose categorical rank is discussed below.

III. Interrelationships of the Mastacembeloidei

In the past a variety of groups have been suggested as close relatives of the mastacembeloids (see Travers, 1984: table II). Although generally recognised as a member of the large and diverse order Perciformes (Regan, 1912 and Greenwood *et al.*, 1966), their interrelationships have remained obscure.

One mastacembeloid synapomorphy (18) occurs in a similar condition in the ammodytoids (excluding *Hypoptychus,* see p. 94). A close phyletic relationship between the mastacembeloids and this group has never been demonstrated and no other congruent apomorphies were found to substantiate a possible close relationship between these taxa. Another mastacembeloid synapomorphy (16) is found in a similar condition among the blennioids (see p. 97). A close phyletic relationship between the mastacembeloids and blennioids was originally proposed by Günther (1861), and has since received support from various authors (see Travers, 1984: table II). However, no further characters were found to substantiate such a relationship. On the contrary this proposal and that relating the ammodytoids to the mastacembeloids are falsified by 6 synapomorphies (19 to 24, and possibly 11 as well) shared with the synbranchoids, and thus indicate a more recent common ancestry for the synbranchoids and mastacembeloids. These 6 synapomorphies are:

19. Loss or reduction in size of the posttemporal bone, accompanied by loss of connection to pectoral girdle.
20. Extension of the dentary posteroventrally along the ventral edge of the anguloarticular.
21. Wide anterolateral face of the ectopterygoid and its direct articulation with the lateral ethmoid.
22. Palatine sutured along the posterolateral face of the vomerine shaft.
23. Insertion of the *levator operculi* muscle on the dorsolateral face of the operculum.
24. Dorsolateral expansion of the *hyohyoidei adductores* muscle, sealing the operculum to the body wall and causing a restricted opercular opening.

Two of these characters are shared uniquely by all mastacembeloid and synbranchoid (20 see p. 98 & 24 see p. 105) species examined. One character (23 see p. 103), apart from occurring in these groups, is also found in two other phylogenetically distantly related taxa. The three remaining characters (i.e. 19 see p. 96; 21 see p. 99 & 22 see p. 102) are not found in all synbranchoids. In those in which they do occur the characters are not generally at such an advanced stage of development as in the mastacembeloids. This may explain the synbranchoid condition of character 11, (the '*musculus intraoperculi*', see p. 104 above).

The phylogeny and systematics of the synbranchoids have been investigated by Rosen & Greenwood (1976). Although these authors found new evidence in support of the placement of these fishes in the Percomorpha, they were unable to offer any evidence of their interrelationships within the group and so retained them in a distinct order, Synbranchiformes. On the basis of the characters discussed above (19–24) I propose that the mastacembeloids, as the sister taxon of the synbranchoids, should be allocated to this order. Independent of my research, Gosline (1983) has recently published evidence that lends support to this proposal. The dissimilarity in the condition of the synapomorphies relating mastacembeloids and synbranchoids (apart from 20 & 24) may indicate an early dichotomy in the genealogical history of the group. Without evidence from fossil remains not even a minimum age of this macroevolutionary dichotomy can be suggested; however, it could be obtained from extrinsic information such as the age of the biogeographical pattern of which these fishes are a part (Humphries & Parenti, in press).

The phyletic affinity of the expanded Synbranchiformes remains uncertain. Berg (1940) suggested a possible relationship between ophicephalids and synbranchids and Travers (1981) noted their possible affinity with the carapids (Ophidiformes: Cohen & Nielson, 1978); a group which, in common with the synbranchids, have a massive ectopterygoid associated with the absence or fusion of the endopterygoid. A comparison between these groups should be the subject of future investigation.

Mastacembeloid intrarelationships

Incorporated in the following analysis are numerous reductional features and absences which are common in several mastacembeloid lineages, particularly those with a small adult size. Features of this type are of doubtful value to phylogenetic analysis when considered individually because they are inclined to occur independently (i.e. convergently) in closely related lineages. However, if two taxa share a unique set of uncorrelated reductional characters, in combination they are reliable evidence (synapomorphies) in support of a monophyletic origin of the group. By necessity, such character sets form a substantial part of this analysis and are discussed in detail below.

I. Character analysis

Osteology

NEUROCRANIUM

In general the mastacembeloid orbital region is characterised by the presence of large pterosphenoids and by their ventromedial connection (Travers, 1984: 14). Although this is the condition in the majority of taxa, the pterosphenoid can occur in two other states. In *Mastacembelus aviceps* (Travers, 1984: fig. 40) the bone is a small splinter-like element sutured along the dorsolateral edge of the frontal. The neurocranium in this microphthalmic species is very small, with many apparently reductional features (discussed below). The condition of the pterosphenoid in *M. aviceps* is intermediate between that in the majority of mastacembeloids and that in *Chaudhuria* and *Pillaia* where it is absent. The secondary loss (i.e. ontogenetic suppression) of the pterosphenoid in *Chaudhuria* and *Pillaia* is a useful synapomorphy of these taxa. The splinter-like pterosphenoid is an autapomorphy of *M. aviceps,* and it may be under similar developmental influences to those which have culminated in the complete loss of the pterosphenoid in *Chaudhuria* and *Pillaia.*

The basisphenoid, too, is absent in *Chaudhuria* and *Pillaia* (Travers, 1984: 53). The lack of a basisphenoid in *Mastacembelus aviceps* and *Mastacembelus crassus* seemingly parallels the condition in *Chaudhuria* and *Pillaia,* and is one of several other parallelisms (discussed below) found only in these taxa among the mastacembeloids I have examined.

A divided posterior end of the parasphenoid is the plesiomorphic condition and occurs in most groups of teleostean fishes. The absence of these processes in the beryciforms (the posterior end of the parasphenoid tapers to a single point along the ventral surface of the basioccipital; Zehren, 1979: 50) appears to be an apomorphic condition.

The basal perciforms ('lower percoids' of Greenwood *et al.*, 1966) typically have the posterior end of the parasphenoid divided into a pair of processes and this is the arrangement in representatives of most perciform groups, including the mastacembeloids.

The basicranium of *Mastacembelus congicus* illustrated by Rosen & Greenwood (1976: fig. 57) inaccurately depicts the posteroventral edge of the parasphenoid as undivided (i.e. in an apomorph condition). The posteroventral region of the parasphenoid in specimens of *M. congicus* is divided into a pair of processes and is similar in this respect to most other mastacembeloid taxa (Travers, 1984: 14).

However, in a number of mastacembeloids the parasphenoid is undivided except for its posterior tip (Travers, 1984: 53). In *Macrognathus* species, *Mastacembelus pancalus* and *Mastacembelus zebrinus* (species F–J in the cladogram Fig. 19 and possibly some or all from the species in the unresolved polychotomy E) the posteroventral face of the parasphenoid is excavated into a blind pit divided medially by a longitudinal ridge. Associated with the deep basicranium in these taxa is a deep exoccipital which has an exceptionally wide ventrolateral face. The deep basicranium with a pitted ventral surface is unique to these mastacembeloids, and is considered to be a synapomorphy uniting this species complex (E–J in cladogram). The fossa accommodating the anterior end of Baudelot's ligament on the posteroventral corner of the basioccipital (Travers, 1984: 70) is particularly deep in these species.

The posterior parashenoid processes in *Mastacembelus sinensis, Chaudhuria* and *Pillaia* are exceptionally long and extend from the region of the parasphenoid adjacent to the lateral commissure to beyond the posterior margin of the basioccipital (Travers, 1984: 53). The relative length of these processes far exceeds that in any other mastacembeloids, and in perciform lineages generally, and is a synapomorphy uniting *Mastacembelus sinensis, Chaudhuria* and *Pillaia* (species complex A–C in the cladogram).

An anterior process on the prootic extending unopposed into the orbital cavity, is a synapomorphy of the mastacembeloids. The anterior process (see p. 91) is absent in *Pillaia, Mastacembelus aviceps* and *Mastacembelus crassus,* giving the bone in these taxa the appearance of the plesiomorphic type. However, the reduced crania (including the loss and reduction of many bones) in these microphthalmic species and their small adult size appear to be indicative of a highly derived state. Thus, the lack of a prootic process would be a secondary loss (i.e. an evolutionary reduction or reversal) rather than a primary absence and one of many such 'apomorphic' losses in these taxa.

The comparatively simple pars jugularis in mastacembeloids is typical of advanced teleosts (p. 91). Among the mastacembeloids a single foramen in the pars jugularis is found only in *Chaudhuria*, *Pillaia* and *Mastacembelus crassus* (Travers, 1984: 67) and is another 'apomorphic reduction' shared by these taxa.

The trigeminal foramen in many mastacembeloids is bordered anteroventrally by a small pedicel that rises from the dorsal edge of the prootic (Travers, 1984: 64). This spur is homologous with a prootic process connected to the tip of a descending pterosphenoid pedicel, anterior to the pars jugularis, in other teleosts (e.g. the 'internal jugular bridge' in labroids; see Rognes, 1973: 69).

The development of this structure has been discussed in detail by Greenwood (1976: 20–27) with respect to its occurrence in the centropomids. Greenwood (1976) found the internal jugular bridge to have a mosaic occurrence among living teleosts, particularly in those with precommissural elongation of the neurocranium. He also showed that the relative contribution of the prootic, pterosphenoid and parasphenoid to the formation of an internal jugular bridge is prone to marked intraspecific variation in *Lates*, and that the pterosphenoid pedicel, or at least the potential to develop it, is primitive for actinopterygians.

Based on this, and the fact that a pterosphenoid pedicel is an integral part of the internal jugular bridge, Greenwood (1976: 27) concluded '...that the bridge too is a primitive feature'.

If an ascending spur is present on the prootic in *Lates* and the other teleosts Greenwood examined it always contributes to the bridge. A prootic ascending spur is present in the majority of mastacembeloids, yet in none does it contribute to the formation of a bridge. This appears to be related to the extreme precomissural elongation of the skull in these fishes (Travers, 1984: fig. 1a to c), and the position of the prootic spur (posterior to the pterosphenoid).

In several mastacembeloids, however, the vessels emerging from the trigeminal foramen are bridged by a type of internal jugular bridge formed by the tip of the prootic anterior process curving anterodorsally (functionally replacing the prootic ascending spur in this respect) and contacting a prominent descending pedicel on the frontal (e.g. *Mastacembelus paucispinis* and *Mastacembelus moorii*; Travers, 1984: 60). In the new species of *Mastacembelus* (Roberts & Travers, in prep.) a narrow ligament runs from the anterior tip of the prootic to the ventral edge of a weakly developed frontal pedicel in much the same manner as the internal jugular bridge ligament described by Greenwood (1976: 22).

The type of prootic/frontal internal jugular bridge occurring in mastacembeloids is not found in any other teleost, which suggests that it is an apomorphic development in these taxa, and possibly a synapomorphy of *M. moorii, M. paucispinis* and *M. sp. nov.*

Apart from these species, an internal jugular bridge type structure was found in *Mastacembelus albomaculatus, M. plagiostomus, M. tanganicae* and *M. congicus*. In these species the bridge may be formed by a pterosphenoid pedicel or by the prootic process alone (Travers, 1984: 60).

Those mastacembeloids in which the prootic ascending spur is reduced or absent from the rim of the trigeminal foramen may be interpreted as exhibiting an apomorphic condition relative to that in which a prominent spur is present. The relatively posterior position of the spur in mastacembeloids indicates that the main region of neurocranial lengthening has been anterior to the lateral commissure (i.e. between the prootic spur and the posterior edge of the orbit) in these fishes.

An extension of the prootic (anterodorsal to the lateral commissure) occurs along the ventral edge of the sphenotic in *Macrognathus* species (Travers, 1984: 68). This flange on the prootic distinguishes these taxa from other mastacembeloids. It borders the upper rim of the trigeminal foramen (to a variable extent); in its most developed state (i.e. *Macrognathus aculeatus*; Travers, 1984: fig. 30a) the flange forms the entire upper rim of the trigeminal foramen. A sequential change in the size of the prootic flange occurs in *Macrognathus aral* and *Macrognathus siamensis,* so that in its least well developed condition it borders only the most posterodorsal margin of the foramen. The presence of this flange is an apomorphic character of *Macrognathus* and is found in a specific state in each of the three *Macrognathus* species.

The saccular otolith in *Mastacembelus brichardi, M. crassus* and *M. aviceps* (Travers, 1984: figs. 39 & 40) is large in relation to that in other mastacembeloids, and is housed in a correspondingly large bullation of the prootic. The large bulla of *M. brichardi, M. crassus* and *M. aviceps* (Travers, 1984: figs. 38–40) is most probably synapomorphic for these species (P, R & S; and possibly *M. latens* [Q], for which no material was available).

The saccular bullae in *Chaudhuria* and *Pillaia* are exceptionally large, with the bulla contained in approximately equal parts in the prootic, exoccipital and basioccipital (Travers, 1984: fig. 15 ai & bi). This arrangement in *Chaudhuria* and *Pillaia* appears to be the plesiomorphic condition (as described in Travers, 1984: 69), but should, perhaps, be interpreted as a redevelopment of the primitive condition (see p. 133 for discussion of reductional trends and 'plesiomorphic mimicry').

In only one of the African taxa, *Mastascembelus micropectus* (a microphthalmic species from Lake Tanganyika; Travers, 1984: fig. 38d), is the large saccular bulla contained in approximately equal parts of the prootic, exoccipital and basioccipital bones.

The dorsal surface of the exoccipital is perforated in *Mastacembelus sinensis, Chaudhuria* and *Pillaia* (Travers, 1984: 69). Although foramina may occur in other mastacembeloids, in none is there the dense perforations typical of these taxa. In addition, the posterior tip of the supraoccipital in *M. sinensis, Chaudhuria* and *Pillaia* separates the dorsomedial margin of the exoccipital from contacting its partner in the midline.

The fact that the exoccipitals in all other mastacembeloids lack a perforated dorsal surface suggests that this character is an apomorphic development in *M. sinensis, Chaudhuria* and *Pillaia.* The posterior extension of the supraoccipital associated with this perforation is an additional synapomorphy uniting these taxa (complex A–C) and is an apomorphy congruent with the very long posterior parasphenoid processes (see. p. 111).

A group of Asian taxa comprising the *Macrognathus* species, *Mastacembelus pancalus* and *M. zebrinus* (and possibly some or all of the species included in polychotomy E) are distinguished from all other mastacembeloids by the steeply sloping dorsal surface of the frontals and extremely narrow neurocrania. Among the examined species showing this trend, it is best developed in *Mastacembelus pancalus* (Travers, 1984: fig. 28a). On account of this and of several other features (e.g. fin length, caudal skeleton and the ratio between the number of abdominal and caudal vertebrae), *M. pancalus* is thought to be the most highly modified of these species. The deeply sloping frontals in *Macrognathus, M. pancalus* and *M. zebrinus* (and possibly some or all species of category E) are a synapomorphy uniting the group.

The frontals in *Chaudhuria* and *Pillaia* (Travers, 1984: 72) lack a descending lamina, another apparently reductional character in these taxa, which does not occur in any other mastacembeloids.

The anterior region of the frontal, roofing the orbital cavity, is reduced in *Mastacembelus brichardi, M. crassus* and *M. aviceps* (p. 138); it is short compared with that in most species. This size reduction in the orbital region of the frontals is a synapomorphic character of these species and one apparently associated with their tendency to be micro- and cryptophthalmic.

In all mastacembeloids apart from *Mastacembelus sinensis* (Travers, 1984: 71), the parietals are separated in the midline by the supraoccipital. The short supraoccipital in this species may not restrict the medial edges of the parietals from contacting one another anteriorly although in some individuals this restriction did occur. Complete medial interparietal contact is a plesiomorphic characteristic of the teleosts (Forey, 1973: 187), and is of wide occurrence. With the exception of the synbranchids (Rosen & Greenwood, 1976), the percomorphs have their parietals separated in the midline by the supraoccipital. It is, thus unlikely that the slight anteromedial parietal contact that may occur in some *M. sinensis* individuals should be interpreted as a plesiomorphic condition. The medial contact of the parietals in *M. sinensis,* is possibly associated with the small size of the supraoccipital in this species.

The cephalic sensory canal system is well developed in all mastacembeloids apart from *Chaudhuria* and *Pillaia.* In *Pillaia* (Travers, 1984: 45) the sensory canals are present, incompletely, in the preoperculum, dentary, frontal, 1st infraorbital and nasal bones, while in *Chaudhuria* (Travers, 1984: 36) they are absent from all cranial bones. The reduction and loss of these canals in *Chaudhuria* and *Pillaia,* appears to represent another synapomorphic secondary loss and part of the evolutionary reduction that characterises these taxa.

JAWS

The upper jaw is composed of a single bone in *Pillaia* (Travers, 1984: fig. 16b), and its shape suggests that it incorporates the premaxilla and the maxilla (Yazdani, 1976). The anterior region of the maxilla in *Mastacembelus aviceps* (Travers, 1984: fig. 44a) is greatly reduced and is tightly connected to the dorsal surface of the premaxilla. This arrangement may serve to illustrate the method by which the pillaiid condition (fused single element) was brought about (see Travers, 1984: 75).

A single upper jaw element was found only in *Anguilla* amongst the outgroups examined. Here, however, the upper jaw is partly fused with the cranium; the maxilla and premaxilla-ethmovomerine bloc having taken over its function (Norman, 1926).

The close association between the maxilla and premaxilla in *M. aviceps* and the fusion between these elements in *Pillaia* are derived modifications autapomorphic for these species.

The size of the premaxillary alveolar surface and the number of teeth it supports vary greatly among mastacembeloids. The premaxillary dentition typical for most taxa consists of an outer row of large caniniform teeth followed by 3 or 4 medial rows decreasing in tooth number and size posteriorly (see Travers, 1984: 76).

Two major modifications of this plesiomorph condition can be recognised. A narrow alveolar surface with only 1–2 inner tooth rows occurs in *Mastacembelus sinensis, Chaudhuria* and *Pillaia* and may be a synapomorphy of these taxa. Conversely the premaxillary alveolar surface is expanded in an assemblage of Asian taxa (Travers, 1984: 76) which includes all *Macrognathus* species, *Mastacembelus pancalus* and *Mastacembelus zebrinus* (and perhaps some or all of the species in lineage E of Fig. 19). In these taxa the alveolar surface extends anterolaterally well beyond the premaxilla and develops a toothed vertical face, the like of which has not been observed in any other teleosts. In other mastacembeloids, as in teleosts generally, an increase in size of the upper jaw dentition always involves the medial expansion of the alveolar surface along its inner edge (as seen in *Mastacembelus moorii*; Travers, 1984: 76) to produce a broad vertical surface toothed on its medial face. Clearly the development of a vertical, anterolaterally extended, premaxillary tooth face is a shared, derived feature of the mastacembeloid taxa in which it is manifest.

In some instances it leads to the development of a series of toothplates which extend along the ventral surface of the large rostral appendage (Travers, 1984: fig. 45b & c), a condition unique to the mastacembeloids and a synapomorphy of those species at present combined generically, mainly because of this feature, in *Macrognathus*. This character can be subdivided into three states each represented by one of the three *Macrognathus* species: *Macrognathus siamensis* has 7–14 rostral toothplates; *M. aral* 14–28, and *M. aculeatus* 38–55 (Roberts, 1980).

There is a distinct morphocline in the anterolateral expansion of the premaxillary alveolar surface ranging from the relatively narrow one in *Mastacembelus keithi* (part of polychotomy E), to the broad surface with numerous (over 50) fragmented rostral toothplates in *Macrognathus aculeatus*.

The posteroventral extension of the dentary below the anguloarticular is a synapomorphy of the mastacembeloids (p. 98). In *Chaudhuria* the ventral edge of the dentary is forked giving rise to a distinctive pair of posteroventral processes (Travers, 1984: 36). This autopomorphic characteristic of *Chaudhuria* distinguishes it from *Pillaia,* with which it shares many apparently synapomorphic features.

The coronoid process on the dentary has been shown to occur in two major conditions, either tall and narrow or short and broad (Travers, 1984: 80). Based on the condition of their coronoid process, the mastacembeloids fall into two major assemblages. These groups, however, are incongruent with the lineages (see Fig. 19) revealed by numerous characters recognized in this study. A parsimonious explanation of this incongruence in the condition of the coronoid processes is suggested by the direct correlation between them and the feeding strategy employed, particularly since the demands of feeding are thought to impose the highest stresses on the cephalic structures of predatory fishes (Osse & Muller, 1980).

Liem (1967) has shown that in the luciocephaloid *Luciocephalus pulcher* the strength of the 'bite', a result of contraction of part A_2 of the *adductor mandibulae*, is enhanced by the height of the ascending (coronoid) process of the dentary. More recently, teleostean modes of feeding have been divided into three major categories (Liem, 1980b) and 'biting' is now considered to be part of the broad, more general feeding strategy of manipulation. The great length of the ascending process on the dentary in *Luciocephalus* increases the torque about the jaw articulation, thereby, providing the greatest mechanical advantage for manipulating prey. This gives a clue to the variation in size of the mastacembeloid coronoid process, particularly as it is short (low/broad) in taxa which have reduced upper jaw bones (e.g. *Macrognathus* species); associated with expansion of the toothbearing alveolar surface, a relatively small A_2 muscle and increased size of the anterior region of the *adductor arcus palatini.* The diet of aquatic insect larvae and oligochaetes (Roberts, 1980) in *Macrognathus* is that expected in fishes with a weak 'bite'. Conversely, those mastacembeloids with a large upper jaw bone (and medially expanded alveolar surfaces), a high (tall/narrow) coronoid process and a well-developed A_2 muscle (e.g. *Mastacembelus mastacembelus* and *Mastacembelus moorii*), are generally predatory piscivores which need a 'bite' of greater strength than do the insectivores.

The length of the coronomeckelian in mastacembeloids has been found to be inversely proportional to the height of the coronoid process on the dentary (Travers, 1984: 81). If coronomeckelian length can be taken as a measure of the size of the A_3 part of the *adductor* *mandibulae* (see Travers, 1984: 125), it may reflect the change in emphasis on particular parts of the adductor musculature with regard to the feeding strategies employed. In species which are principally insectivorous (e.g. *Macrognathus*) and have a relatively weak 'bite' there is a greatly developed coronomeckelian and A_3 part of the *adductor mandibulae.* The size and the strength of these elements may help to increase the efficiency of the high speed inertial suction mode of feeding probably employed by such fishes when capturing small prey or food. In contrast, when mastacembeloids capture large prey or food items (i.e. predaceous piscivores such as *M. mastacembelus* and *M. moorii*) they firmly grasp and bite the prey until it is rendered (by being broken down to a smaller size and/or correctly positioned) to a state which, with the aid of inertial suction, can be readily engulfed. The initial manipulation of large prey or food requires a 'bite' of greater strength (produced by the larger height—tall/narrow—of the coronoid process and relatively great size of part A_2) for grasping and biting, and places less reliance on inertial suction as the major mode of feeding, thus obviating to some extent the need for a very long coronomeckelian and a well-developed A_3 *adductor mandibulae* muscle.

A group of taxa with a low/broad coronoid process may be distinguished by the posterior encroachment of the toothbearing alveolar surface on the dentary, across the medial face of the coronoid process (Travers, 1984: 80). This development is considered to be apomorphic, as no outgroup taxa had a toothed medial face of the coronoid process. It is another synapomorphy of the Asian mastacembeloid lineage comprising the *Macrognathus* species, *M. pancalus* and *M. zebrinus* (and possibly some or all of those species in polychotomy E of Fig. 19), and is evidence in support of the monophyletic origin of this Asian lineage since it is congruent with similar indications provided by the anterior expansion of the premaxillary alveolar surface (see above p. 114).

A large, dorsally situated coronomeckelian is a synapomorphy uniting most mastacembeloids. However, in *Chaudhuria* and *Pillaia* (Travers, 1984: 80) it is a small ossicle on the medial face of the anguloarticular, posterodorsal to Meckel's cartilage, and resembles the plesiomorphic condition seen in such groups as the percoids.

The variable size of the coronomeckelian in all other mastacembeloid taxa has been functionally related to the size of the coronoid process on the dentary (p. 114). The small coronomeckelian in *Mastacembelus brachyrhinus, M. brichardi, M. aviceps* and *M. crassus* (and possibly *M. latens* as well—species O to S in cladogram), however, is much smaller than would be expected from the height of the coronoid processes in these taxa. The condition is exceptional among mastacembeloids, and rather than being related to the jaw mechanism (e.g. height of coronoid process) would appear to be governed by the reductional trend characterizing many other features of their anatomy, and is presumably another synapomorphy uniting these species. However, even in its reduced state it represents a condition that is derived relative to that in the outgroup taxa examined.

The condition of the coronomeckelian in *Chaudhuria* and *Pillaia,* which also demonstrate several reductional features could be truly plesiomorphic. However, this explanation is less parsimonious than the alternative view that, the coronomeckelian in *Chaudhuria* and *Pillaia* has been secondarily reduced.

The absence of a coronoid process on the anguloarticular in the majority of mastacembeloids has been discussed in the previous section (p. 99), and is a plesiomorphic feature. The low, broad-based coronoid projection on the anguloarticular in *Mastacembelus zebrinus, M. pancalus* and all *Macrognathus* species, thus distinguishes them from all other mastacembeloids. Its development in these species is considered to be derived in a manner similar to that described by Rosen & Greenwood (1976: 46) for a coronoid process on the anguloarticular in two synbranchid taxa.

Macrognathus is also distinguished from all other mastacembeloids by the anterior position of the facet that notches the dorsal edge of the anguloarticular (Travers, 1984: 82). In all other species the facet occurs on the posterodorsal edge of the bone. Although the position of the facet is subject to variation amongst the percomorphs, it generally lies on the posterodorsal edge of the anguloarticular, especially if there is a large coronoid projection. The position of the facet in *Macrognathus* is, therefore, considered to be an apomorphic feature.

THE PTERYGO-PALATINE ARCH

In most mastacembeloids the metapterygoid is widely separated from the anteroventral edge of the hyomandibula. The symplectic in these taxa is a long bone which often has an irregular dorsal lamina whose upper edge contacts the ventral edge of the metapterygoid (Travers, 1984: 82).

In *Mastacembelus sinensis, Chaudhuria* and *Pillaia,* however, the symplectic is smaller than in most other mastacembeloids, and the metapterygoid and hyomandibula are in contact.

Of these two conditions, the latter is the more common being widely found among higher neoteleostean fishes, occurring even in those which have a large symplectic (e.g. *Ophidion rochei* and *Carapus acus,* Fig. 14a; *Congrogadus subduceus,* Fig. 9; *Notothenia sema,* Fig. 14b; *Eliotriodes sexguttatus,* Fig. 14c; *Luciocephalus pulcher,* Fig. 14d).

Thus, the contact between the hyomandibula and metapterygoid in *M. sinensis, Chaudhuria* and *Pillaia* more closely approximates to the arrangement of these bones in other neoteleosts than does the wide separation of the hyomandibula and metapterygoid characteristic of the other mastacembeloid taxa. On this basis the arrangement in *M. sinensis, Chaudhuria* and *Pillaia* is thought to represent the plesiomorphic condition, (alternatively, it could be a secondary redevelopment that simply mimics it), whilst the wide separation between these bones is a synapomorphy of all other mastacembeloids (the Asian and the African species D–S in Fig. 19).

The size and shape of the endopterygoid is highly variable among neoteleosts, and the bone may even be absent.

The mastacembeloid endopterygoid also varies in shape and size (Travers, 1984: 83) but generally it lies dorsal to the quadrate, its anterior end overlying the posterodorsal edge of the ectoperygoid, and its posterior end overlapping the anterodorsal edge of the metapterygoid. The posterior end of the endopterygoid is often subdivided into blunt, posteromedially directed processes. Fibres of the *adductor arcus palatini* muscle merge into short tendons which insert on the tips of these processes. Since this state most closely resembles that in other percomorph lineages, it is thought to represent the plesiomorphic condition of the mastacembeloids.

A boomerang-shaped endopterygoid occurs in a group of Asian mastacembeloids including *Mastacembelus mastacembelus, M. armatus, M. erythrotaenia, M. oatesii, M. unicolor* and possibly *Mastacembelus alboguttatus* (for which no material was available), i.e. the species forming D in cladogram. The posterior arm of the endopterygoid in these species has an undivided tip that extends across the quadrate/metapterygoid junction; the anterior arm is larger than the posterior arm, and extends between the ectopterygoid/lateral ethmoid point of articulation. The anterior elongation of the endopterygoid is an apomorphic development, and provides a synapomorphy uniting *M. mastacembelus, M. armatus, M. erythrotaenia, M. oatesii, M. unicolor* and possibly *M. alboguttatus.*

A very small splinter-like endopterygoid is a characteristic feature of the suspensorium in *Mastacembelus brichardi, M. aviceps, M. crassus* and probably in *M. latens* (Travers, 1984: 83). The small size of the bone may be a secondary reduction and would, in that case, be a synapomorphic character uniting these species (species P–S in Fig. 19). The absence of an endopterygoid in *Mastacembelus sinensis, Chaudhuria* and *Pillaia,* may be the culmination of this trend, in which case it is a synapomorphy for these taxa.

In *Chaudhuria* and *Pillaia* no palatine could be identified and it may be fused with the ectopterygoid, a fusion which could account for the particularly long anterodorsal arm of the ectopterygoid in these species (Travers, 1984: fig. 17a & b).

The medial face of this long anterior arm does not articulate with the lateral ethmoid in *Chaudhuria* and *Pillaia.* Instead, it lies along the posterolateral face of the vomerine shaft. The narrow lateral face of the ectopterygoid, its long anterodorsal arm connected to the

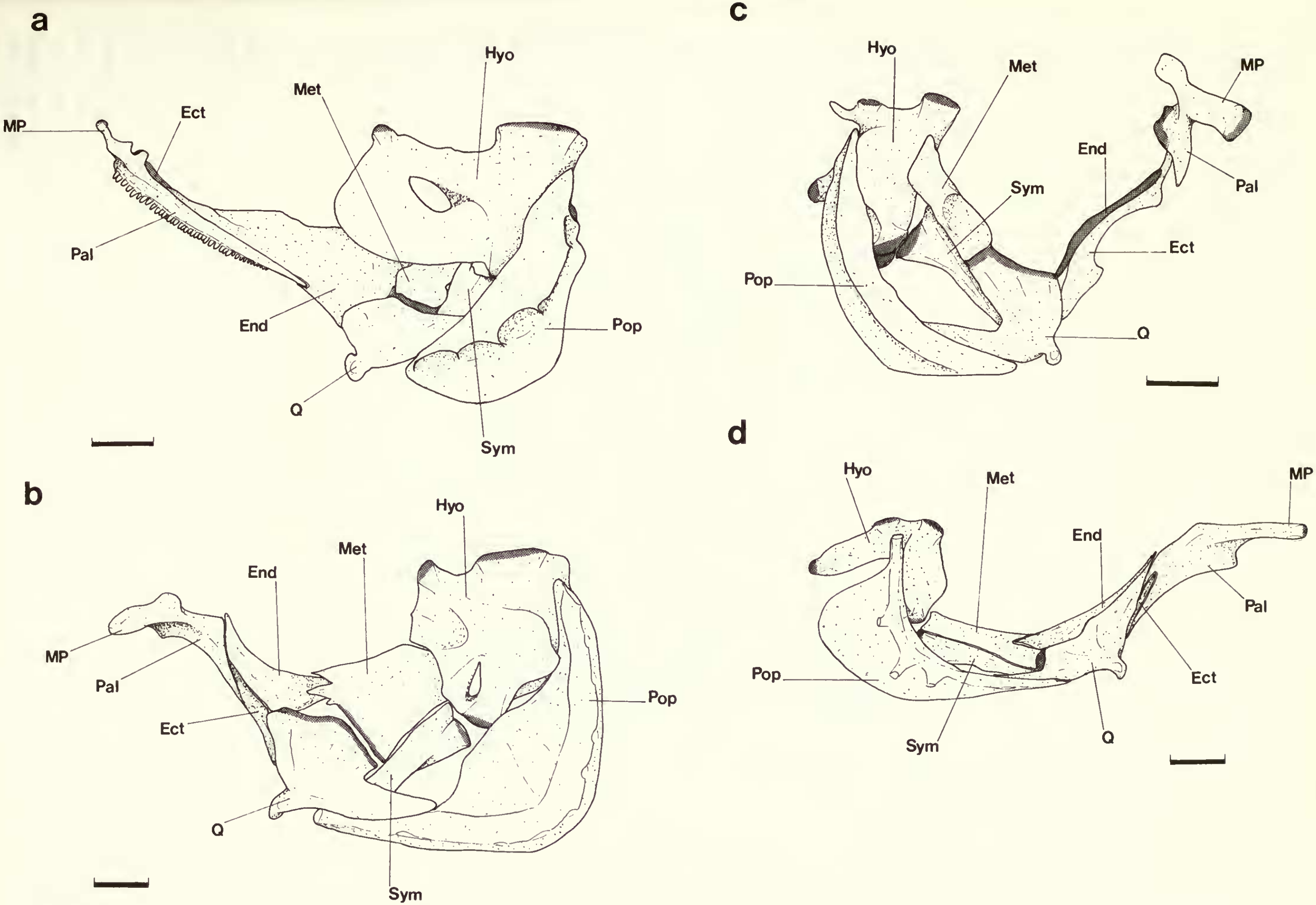

Fig. 14 Lateral view: left hyopalatine arch and preoperculum in (a) *Carapus acus* and (b) *Notothenia sema*; right hyopalatine arch and preoperculum in (c) *Eleotriodes sexguttatus* and (d) *Luciocephalus pulcher*.

vomerine shaft, and the loss (or fusion) of the palatine, are all synapomorphic characters uniting *Chaudhuria* and *Pillaia*.

The relatively narrow lateral face and long anterodorsal arm of the ectopterygoid in *M. sinensis*, would seem to represent an intermediate stage of character transformation between that found in the majority of mastacembeloids and that in *Chaudhuria* and *Pillaia*. The small size of the palatine, which does not extend posteriorly into the orbital cavity in *M. sinensis*, also appears to be an intermediate condition between the two groups. Although the lack of a deep anterolateral face on the ectopterygoid in *M. sinensis, Chaudhuria* and *Pillaia* may be plesiomorphic (relative to the usual mastacembeloid condition), associated as it is with the loss of direct articulation between the lateral ethmoid and the palatine, it is considered to be derived, through reduction from that in the majority of mastacembeloids. Thus, it too is a synapomorphy for the three taxa.

An ectopterygoid with a narrow lateral face (relative to that in the majority of species), but lacking a great increase in the length of its dorsal arm and reduction or loss of the palatine, occurs in *Mastacembelus aviceps, M. crassus* and possibly *M. latens*. The small lateral face of the ectopterygoid in these species could be at an intermediate stage in the reductional trend culminating in the condition seen in *Chaudhuria* and *Pillaia*. If this is the case it is a synapomorphy uniting *M. aviceps* and *M. crassus* (R & S in Fig. 19).

The anterior edge of the quadrate is approximately straight in the majority of the mastacembeloids (Travers, 1984: 83). In *Macrognathus, Mastacembelus pancalus* and *M. zebrinus* (and possibly part or all of polychotomy E) it is deeply indented across the particularly large posteromedial processes on the ectopterygoid. This indentation of the quadrate is considered to be a synapomorphy for these species (F–J in Fig. 19).

A round facet on the posteromedial margin of the ectopterygoid articulates with a similar facet on the anterolateral margin of the quadrate in *Mastacembelus pancalus* (Travers, 1984: 83). An articulatory facet between these bones is not found in any other mastacembeloids, and is thus an autapomorphy which may be associated with the very deep anterolateral face of the ectopterygoid in *M. pancalus*.

A small and weak ascending spur present on the palatine in the majority of mastacembeloids is the only remnant of the plesiomorph condition in which the bone is connected to the lateral ethmoid (see discussion on p. 102). In some Oriental species (*Macrognathus* species, *Mastacembelus pancalus* and *M. maculatus*) even this spur is absent, a condition representing the culmination of a trend in mastacembeloids leading to the complete loss of the palatine (as in *Chaudhuria* and *Pillaia*). The loss of the palatine spur also occurs, mosaically, among the African mastacembeloids (see Travers, 1984: 86) and must be considered a trend independent of that in *Macrognathus, Mastacembelus pancalus* and *M. maculatus*. Thus, its loss is treated in each instance as an apomorphic feature, and one that appears to have occurred independently on several occasions. If the lack of the spur in *Macrognathus* species and *Mastacembelus pancalus* is considered as a synapomorphy of these taxa, it adds support to two other synapomorphies (discussed below—see p. 118 & 123) that unite them.

OPERCULAR SERIES

The lateral face of the mastacembeloid preoperculum is pierced by 4 or 5 sensory canal pores in the majority of taxa (Travers, 1984: 86). Five preopercular sensory canal pores occur commonly among many perciform assemblages, including the blennioids, gobioids and a variety of percoid families, for example pseudochromids (*sensu* Springer, Smith & Fraser, 1977), percoids, cichlids and cepolids; this most probably represents the plesiomorphic condition. A decrease in the number of these pores, therefore, is an apomorphic tendency.

Such an apomorphy is found among certain mastacembeloids (Travers, 1984: 86), including an assemblage of at least 13 African species (the polychotomous species complex L) as well as in species M–S (see Fig. 19).

A reduction in the number of pores is carried to an even greater extreme among what appears to be a sublineage of the assemblage containing the polychotomy L and species M to S. In the latter there is a sequential loss of sensory canal pores from 5 in *Mastacembelus paucispinis* and the undescribed *Mastacembelus* species (the model number for the assemblage containing both polychotomy L and species M to S) to 4 in *Mastacembelus brichardi,* 3 in *Mastacembelus brachyrhinus,* and finally 2 in *Mastacembelus crassus* and *Mastacembelus aviceps* (Travers, 1984: fig 44a & b). If loss of preoperculum sensory canal pores is considered as a synapomorphy which can occur in several states (i.e. 4, 3 or even 2 pores) each of which is apomorphic for a particular species, the trend could be cited as evidence supporting a monophyletic origin for the species in which it occurs. This hypothesis is also supported by a similar sequential decrease in the number of caudal vertebrate in *Mastacembelus paucispinis,* the undescribed *Mastacembelus* species, *M. brachyrhinus, M. brichardi, M. aviceps* and *M. crassus* (see p. 126), and by the absence of a toothplate on hypobranchial 3 in these species (discussed on p. 124).

Five preopercular pores generally are present in the majority of the other African species (the ill-defined complex K in Fig. 19). However, 7 species in this complex have 4 pores (see Travers, 1984: 86) and, on the basis of this character, these species should be more closely related to species in polychotomy L and to species M to S than to other members of complex K.

So far no character has been found to unravel the interrelationships of the 4–pored species tentatively included in complex K. There are, however, a number of synapomorphies (not found in complex K) which unite the species included in the assemblage comprising polychotomy L and species M to S. Thus, for the time being, the presence of only 4 preopercular sensory canal pores in certain members of complex K must be considered an independently acquired character.

The upper preopercular sensory canal in *Mastacembelus crassus* and *M. aviceps,* instead of opening at the dorsal tip of the preoperculum, opens along its posterodorsal edge. This positioning of the preopercular canal was not found in any outgroup taxa and is considered to be synapomorphic for these species.

In *Macrognathus* and in *Mastacembelus pancalus* the three central pores open from the tip of short, descending branches of the main preopercular canal (Travers, 1984: fig. 45b & c). This branching of the canal is probably correlated with the wide lateral face of the preoperculum in these taxa. In representatives from a number of perciform lineages including the percoids (e.g. the cichlids *Astatotilapia burtoni* and *Crenicichla alta* and to a lesser extent the pseudochromid *Pseudochromis caudalis*) the preopercular sensory canal may also be branched. This independent development of a branched sensory canal appears, in each instance, to be an apomorphic feature. Its development in *Macrognathus* and *M. pancalus* alone amongst mastacembeloids strongly suggests that it is a synapomorphic feature for these two taxa and may be used as further evidence in support of the view, proposed earlier, on the basis of other features (p. 118), that *M. pancalus* is more closely related to *Macrognathus* than to any other mastacembeloid.

HYOID AND BRANCHIAL ARCHES

The anterior ceratohyal is connected to the posterior ceratohyal by a series of interdigitating dentate sutures in all mastacembeloids, apart from *Chaudhuria* and *Pillaia* (Travers, 1984: 87). In *Mastacembelus sinensis* these processes are relatively short, irregularly positioned spikes (Travers, 1984: fig. 51) that extend into the cartilaginous interface only. A single flange extends from the anterior to the posterior ceratohyal in *Chaudhuria* and *Pillaia* (Travers, 1982: fig. 19a & b) but otherwise the bones are connected by a straight cartilaginous suture.

A straight suture is the arrangement found in most teleosts below the acanthomorph level I have examined. The development of interdigitating dentate processes connecting the two ceratohyals occurs mosaically among phyletically diverse higher acanthomorph lineages and even among closely related taxa. For example, among the illustrations of various paracanthopterygian hyoid arches shown by Rosen & Patterson (1969), in only one batrachoid species (*Thalassophryne megalops*; fig. 57a) are the anterior and posterior ceratohyal shown as connected by interdigitating processes. More recently, Zehren (1979) has described the osteology of nine beryciform families and in only one—Berycidae—are the ceratohyals connected by interdigitating processes. Among the percoids there is considerable variation in the way the ceratohyals are interconnected. This is shown by MacDonald (1978) in the Percichthyidae; in some (e.g. *Maccullochela peeli*) there is a large interdigitating process whilst in others (e.g. *Macquaria australasia*) the connection is by a straight suture. A similar situation is shown in different nandid genera by Liem (1970). The centropomids on the other hand, when viewed laterally, have a straight suture (as illustrated by Greenwood, 1976: fig. 20), but in medial view a number of small interdigitating processes can be seen.

In the synbranchids (Rosen & Greenwood, 1976: figs. 25 & 42 to 50) the ceratohyals are always connected by large dentate sutures.

Although the development of (or at least potential to develop) interdigitating ceratohyal processes is apomorphic for acanthomorph fishes, the mosaic distribution of this character makes it of limited taxonomic value.

The arrangement of the anterior and posterior ceratohyal in *M. sinensis, Chaudhuria* and *Pillaia* resembles, to some extent, the plesiomorphic condition but it is most probably a result of the interdigitating process having been secondarily lost and may be considered as a further synapomorphy of these highly derived taxa.

Basibranchial 1 in mastacembeloids has a deep ventral keel in all taxa except *Mastacembelus sinensis, Chaudhuria* and *Pillaia* (Travers, 1984: 90). An outgroup survey of this character reveals that it has a similar mosaic distribution to that of the ceratohyal suture described above. For example, a keel of relatively small proportions (compared with that

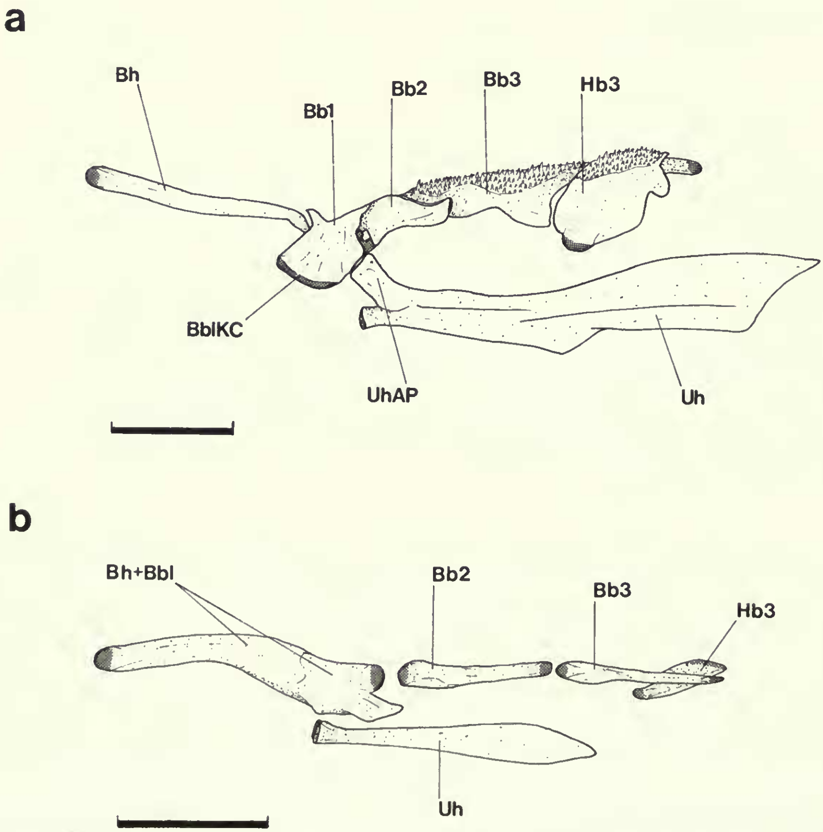

Fig. 15 Basibranchial/urohyal arrangement in: (a) *Carapus acus*; (b) *Synbranchus marmoratus*, lateral aspect, left side.

in the mastacembeloids) occurs on basibranchial 1 in the ophidioids (e.g. *Carapus acus* Fig. 15a); the synbranchids have a well developed keel that extends posteriorly below the anteroventral surface of basibranchial 2 in most taxa (e.g. *Synbranchus marmoratus* Fig. 15b), as do many perciforms, although it is low in sphyraenoids, trachinoids, anabantoids and channoids.

The flat ventral surface of basibranchial 1 in *M. sinensis, Chaudhuria* and *Pillaia* resembles the plesiomorphic condition, and could be either primarily plesiomorphic or a secondary redevelopment of that condition. The arrangement of the keel in *Mastacembelus aviceps* and *Mastacembelus crassus* (Travers, 1984: fig. 55) may help to resolve this problem. In these species, although the keel is present, it is much smaller than that in the other mastacembeloids. On the basis of many other characters, *M. aviceps* and *M. crassus* can be considered highly derived species exhibiting several features in a somewhat reduced state and intermediate between the modal condition and that in *Chaudhuria* and *Pillaia*. The low keel on basibranchial 1 in *M. aviceps* and *M. crassus* may be such a character. If, during evolution, reduction of the keel has occurred in these mastacembeloids, the arrangement of the keel in *M. sinensis, Chaudhuria* and *Pillaia* could well be the result of a similar trend,

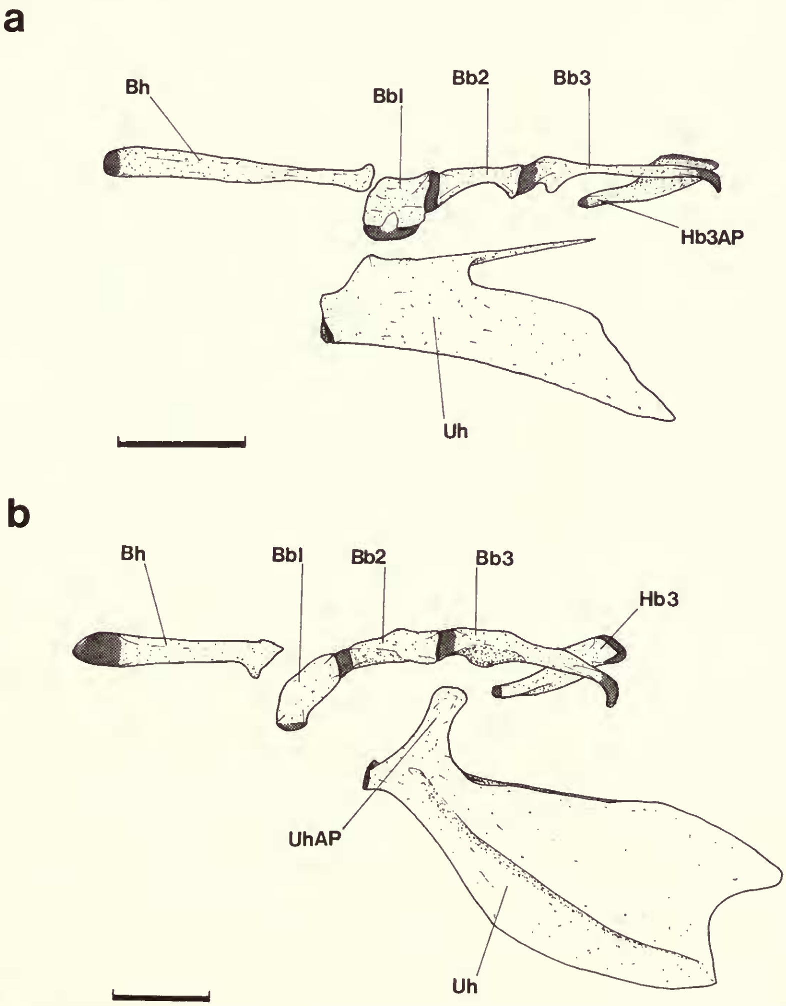

Fig. 16 Basibranchial/urohyal arrangement in: (a) *Lepomis macrochirus*; (b) *Scorpaenodes insularis*, lateral aspect, left side.

independently occurring in these taxa, and which has resulted in the complete loss of the keel.

The ventral edge of the keel on basibranchial 1 is cartilaginous in some mastacembeloids, and is correlated with the direct articulation of this bone with the urohyal. A faceted dorsal surface on the urohyal, or some form of ascending process generally articulating directly with basibranchial 1, is a characteristic feature of all Asian mastacembeloids apart from *Chaudhuria* which in this respect is similar to the African species (in all the urohyal lacks an ascending process or any form of articulation with basibranchial 1). A similar articulation is widespread among many perciform lineages and is particularly common among percoid families, (e.g. centropomids, percids, nandids, teraponids, cichlids, gadopsids and cepolids). The shape of the urohyal and its ascending process in these taxa is often specific to the family, as for example in the teraponids (Vari, 1978). In the centrarchids (e.g. *Lepomis macrochirus* Fig. 16a) the ventral edge of basibranchial 1 is cartilaginous, and articulates synchondrally with the urohyal in much the same manner as it does in some mastacembeloids (e.g. *Macrognathus* species). The scorpaeniforms also show a direct connection between the anterodorsal edge of the urohyal and basibranchial 1 (Fig. 16b).

The urohyal in beryciforms was found by Zehren (1979), to bear '. . . a short but distinct dorsally directed process for attachment of ligaments from the tips of the third hypobranchials'. I have found a similar arrangement of ligaments between hypobranchial 3 and the urohyal in the gadiforms (e.g. *Gadus morhua*) and ophidiforms (e.g. *Ophidion rochei* Fig. 17a), whereas the argentinoids (e.g. *Argentina silus* Fig. 17b) have the posterior end of their

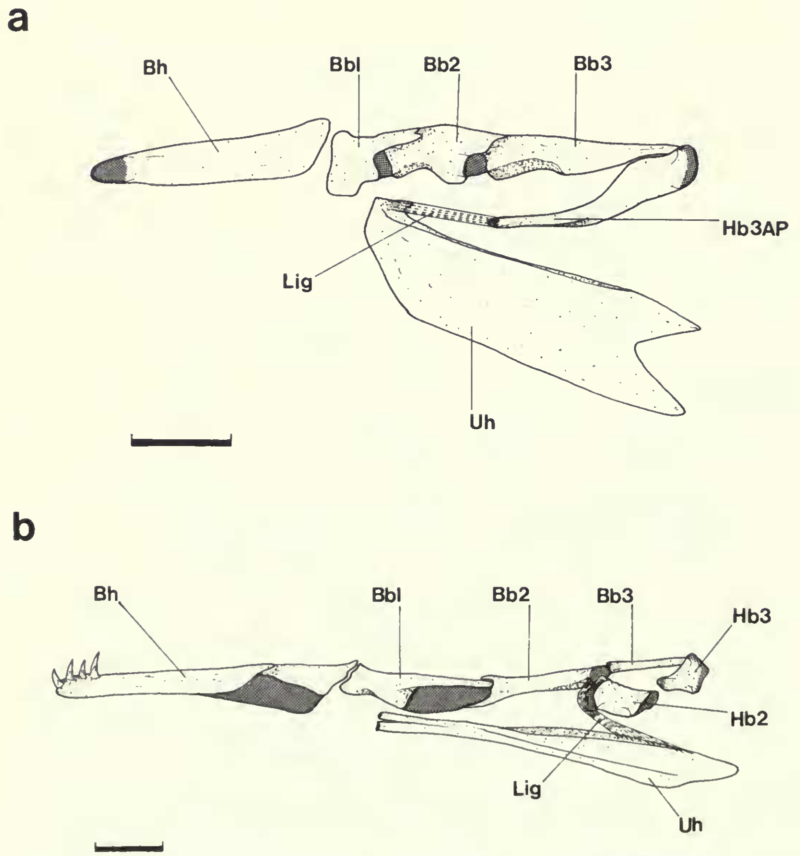

Fig. 17 Lateral view of the basibranchial/urohyal arrangement (left side) in: (a) *Ophidion rochei* (with ligamentous connection to hypobranchial 3); (b) *Argentina silus* (with ligamentous connection to hypobranchial 2).

long urohyal (which lacks an ascending process) ligamentously connected to the anterior tips of the second hypobranchials.

Among neoteleosts the development of an ascending process on the dorsal edge of the urohyal appears to be primitively associated with a ligamentous connection to the anterior tips of the third hypobranchials. During the course of neotelostean evolution these ligaments may have shifted their anterior connection from the urohyal to the basibranchials. Thus, the anterodorsal process on the urohyal, once freed from its ligamentous connection to the third hypobranchials, could become associated with the ventral surface of basibranchial 1. This developmental trend may result in the synchrondral articulation found between the keeled ventral edge of basibranchial 1 and the urohyal in various perciform taxa, including some mastacembeloids (e.g. *Macrognathus* species and *M. pancalus*) and such percoids as the centrarchids (e.g. *Lepomis macrochirus*).

An ascending process on the urohyal ventral to basibranchial 1 is widely distributed among many outgroups I have examined, as well as in most Oriental mastacembeloids, where it appears to be a retained plesiomorphy. This interpretation is consistent with the view expressed by Stiassny (1981: 98) that the urohyal ascending process is plesiomorphic in cichlids. Among Asian mastacembeloids the development of a direct articulation between the urohyal and basibranchial 1 is a derived condition, and is a synapomorphic feature of *Macrognathus* species and *Mastacembelus pancalus* (G–J in Fig. 19). This feature is another character indicating that *M. pancalus* is more closely related to *Macrognathus* species than to any other mastacembeloids.

The ascending process on the urohyal in *Mastacembelus sinensis* is connected to the ventral face of basibranchial 2 (Travers, 1984: fig. 52a) and is somewhat like the arrangement in *Mastacembelus zebrinus,* in which the long ascending process lies along the posterior edge of the keel on basibranchial 1 and has its tip connected to basibranchial 2 (Travers, 1984: fig. 52b). The unusual condition of the urohyal in these species appears to be autapomorhic for each. A low dorsal ridge on the urohyal in *Pillaia* (Travers, 1984: 46) lies below the ventral face of basibranchial 2 but a pair of ligaments from the anterior tips of the 3rd hypobranchials insert on the ridge's posterior edge, replicating the plesiomorphic condition.

The lack of an ascending process on the urohyal (or any form of direct articulation between it and basibranchial 1) is unique to *Chaudhuria* amongst the Asian taxa; most probably, having been secondarily lost it is an apomorphic feature that is convergent with the arrangement of the urohyal in the African mastacembeloids. For the African assemblage too, this character is a synapomorphy and may be cited as further evidence in support of their monophyletic origin.

The ventral processes on basibranchial 2 occur in two states that are of value in defining sublineages within the mastacembeloids. One of these states involves the anterior extension of the tip of the processes to a point where they form an arch over the first afferent branchial artery, and the connection by a short ligament, of each process to the posteroventral margin of the keel on basibranchial 1 (Travers, 1984: 92). Such arched processes are found only in some species of the assemblage which is also characterised by its members usually having fewer than 5 preopercular sensory canal pores (species complex L; see p. 118). In this assemblage the species with arched processes on basibranchial 2 are provisionally grouped into an unresolved polychotomy (termed L; see cladogram) because no characters have been found which can be used to resolve their interspecific relationships. In the second state basibranchial 2 lacks ventral processes. This is a condition found only in *Mastacembelus aviceps* (and possibly *M. latens), in Mastacembelus sinensis, Chaudhuria* and *Pillaia.* Although the condition of basibranchial 2 in these taxa resembles the plesiomorphic state, it is not necessarily a true plesiomorphy. *Mastacembelus aviceps* has been shown by numerous characters to be more closely related to the Zairean species *M. crassus* and *M. latens,* than to any other taxa. Similarly, *M. sinensis, Chaudhuria* and *Pillaia* appear to form a closely related group. Thus, the lack of ventral processes on basibranchial 2 in these taxa must be interpreted as a secondary, thus apomorphic loss which has occurred independently in both Asian and African groups.

Nelson (1969) first convincingly demonstrated a general evolutionary trend in teleostean gill arches towards the development of specialised structures by fusion and loss of dermal and endochondral elements.

The mastacembeloid gill arches lend support to his views, in particular the dorsal gill arch elements which have no uncinate process on the first or second epibranchial, lack a first and fourth pharyngobranchial (although the fourth toothplate is present), and have only a very small second pharyngobranchial with an equally small toothplate. This is the condition of the dorsal gill arches in most species.

The absence of fused toothplates on pharyngobranchial 2 is a further apomorphic development, and a synapomorphy for a group of African species comprising all those grouped in polychotomy L (on the basis of their arched basibranchial 2 ventral processes) and species M to S (see cladogram Fig. 19). The lack of a fused toothplate on pharyngobranchial 2 corroborates the evidence cited in support of the monophyletic origin of these taxa (see p. 119), and indicates the occurrence of a major dichotomy among African mastacembeloids.

The reductional trend involving pharyngobranchial 2 (i.e. the loss of its toothplate) culminates in the complete loss of the bone in one specimen of *Pillaia indica,* although in another specimen a well developed pharyngobranchial 2 is present. *Chaudhuria* and *Pillaia* both lack pharyngobranchial 2 toothplates, in this respect being convergent with the African taxa discussed above.

The ventral gill arch elements are also prone to reduction, by fusion or loss of dermal and endochondral elements. Such an apomorphic trend in the mastacembeloids involves the loss of an anterior process on hypobranchial 3 together with the loss of the ligaments connecting it to basibranchial 2.

A long anteroventral process on hypobranchial 3 typically occurs in most groups of higher euteleostean fishes. In some representatives of these groups there is what appears to be a loss of these processes, as shown for example in the synbranchids (Rosen & Greenwood, 1976: compare fig. 43 of ventral gill arch skeleton in *Ophisternon bengalense* with fig. 50 of the same elements in *Monopterus cuchia*). This situation is convergent with that in some mastacembeloids.

The lack of an anterior process on hypobranchial 3 is another synapomorphy uniting those mastacembeloids which have arched ventral processes on basibranchial 2 (p. 123), and provides further evidence in support of their monophyletic origin (i.e. complex L: Fig. 19).

If a fused toothplate on the dorsal surface of hypobranchial 3 is a synapomorphy of the mastacembeloids (p. 103) its absence in some taxa must be interpreted as a secondary loss. The fact that the toothplate is generally absent in those lineages characterised by reductional trends (e.g. *Pillaia* and *Mastacembelus paucispinis,* the undescribed *Mastacembelus, M. brachyrhinus, M. brichardi, M. aviceps* and *M. crassus*) lends weight to the view that its absence is a secondary loss.

The toothplate is also absent in five other species, namely *Mastacembelus mastacembelus, M. marmoratus, M. niger, M. sclateri* and *M. ubangensis,* the last four of which have been tentatively included in assemblage L. This assemblage is thought to be the sister group of species M to S (as they share the absence of a fused toothplate on pharyngobranchial 2, and have 4 or fewer preopercular sensory canal pores). The overlap in this character between some species in L and species M to S (for which it is a synapomorphy) serves to illustrate the point that further study may well reveal more complex interrelationships between these groups. The lack of a fused toothplate on hypobranchial 3 in *M. mastacembelus* (a species showing few reductional features) must presumably represent a further independent, secondary loss of this character convergent with that in *Pillaia* and the African species. However, in view of its rather mosaic distribution it is perhaps best not to rely too heavily on this character.

PECTORAL GIRDLE

The ability to burrow into the substrate is a phenomena independently acquired in a number of percomorph fishes, including the synbranchoids (Lüling, 1980), blennioids (Springer,

1968) and mastacembeloids. However, not all mastacembeloids burrow (Schofield, 1962) and in those that do (including *Mastacembelus zebrinus, M. pancalus* and the 3 *Macrognathus* species) this ability could be an underlying synapomorphy of the group. However, until more is known of the burrowing habits of all mastacembeloids, particularly the African taxa, a final decision cannot be made on its value as an indicator of phyletic relationships.

When burrowing, mastacembeloids employ a rapid side-to-side movement (pers. obs.) of a kind not described for any other burrowing species. This mechanism may account for the development of a large ventral limb of the cleithrum with a wide lateral face (presumably for extra muscle attachment) in *Mastacembelus zebrinus, M. pancalus* and the *Macrognathus* species (Travers, 1984: 98). This feature is a synapomorphy of these taxa (species F to J in Fig. 19). In no other mastacembeloid taxon is a cleithrum of these proportions found.

Development of the cleithrum has been taken a stage further in *Mastacembelus zebrinus* (taxon F in cladogram). Here it has a particularly wide ventrolateral face protracted anteroposteriorly and connected with its opposite number medially to give the pectoral girdle a deep, 'keeled' appearance (Travers, 1984: fig. 67). This arrangement of the cleithrum is a species specific characteristic of *M. zebrinus*.

A reverse trend is seen in some species. The cleithrum is very slight in the highly derived species *Mastacembelus brichardi, M. aviceps* and *M. crassus* (and probably *M. latens*). This appears to be another evolutionary reduction associated with the small size of these micro- and cryptophthalmic species, and as such is treated as a synapomorphic character indicative of their shared recent common ancestry.

This trend is taken even further in the Tanganyikan *M. micropectus* which, as its name implies, has particularly small pectoral fins that may even be completely lacking from some individuals (pers. obs. and D. J. Stewart pers. comm.). *M. sinensis* and to a greater extent *Chaudhuria* and *Pillaia* also have small pectoral fins, but larger than those in the Zairean rapids species and *M. micropectus*.

The endemic species from the lower Zairean rapids and *Mastacembelus sinensis, Chaudhuria* and *Pillaia* from Asia, are characterised by numerous derived reductional features which have generally been treated severally as synapomorphies in this study. It could be argued that such an interpretation is incorrect on the grounds that they are inevitable consequences correlated with the small adult size reached by these taxa (i.e. paedo- or peramorphosis; Gould, 1977; Alberch, 1979; Fink, 1982). This, however, would be a gross oversimplification of the complex interaction of extrinsic (e.g. the highly specialised rapids environment) and intrinsic (e.g. genetic, hormonal or cellular) influences (morphogenetic processes) that appear to be moulding the morphology of these taxa which, anyhow, can in at least one species, have an adult size comparable to that reached by other mastacembeloids, from both Asia (e.g. *Mastacembelus maculatus*) and Africa (e.g. *Mastacembelus shiranus*), but which lack reductional features.

Primitively, the scapula is pierced by a large foramen in representatives from most major euteleostean lineages. In the more derived fishes, development of the foramen is known to follow various trends including its subdivision (e.g. in a number of beryciform families; Zehren, 1979), and its anterior migration. This migration results in the anterior border of the foramen becoming surrounded by the cartilage which lines the anterior edge of the scapula. A change in the position of the scapula foramen in this manner can be seen in a variety of perciform assemblages, including the mastacembeloids. The foramen lies across the anterior border of the bone and its cartilage surround in all African mastacembeloid taxa (Travers, 1984: 100), whereas, in all Oriental species, including *Mastacembelus sinensis, Chaudhuria* and *Pillaia*, the foramen is completely bone enclosed. Of these two conditions the former is the more derived and is a synapomorphy supporting the hypothesised monophyly of the African assemblage.

VERTEBRAL COLUMN

In all mastacembeloids, other than those with relatively low vertebral counts, an increase in the total number of vertebrae does not occur equally among abdominal and caudal elements; the number of caudal vertebrae is generally the greater by a count of 15–20.

With few exceptions, the African species have a proportionally larger number of caudal vertebrae when compared with the Asian lineages (Travers, 1984: 107). The increased number of caudal vertebrae in these African species is presumably an apomorphic development, and a further synapomorphy of this group.

If the several exceptional African species, which in contrast have a relatively low number of caudal (as opposed to abdominal) vertebrae, are arranged in order of their decreasing vertebral number, the sequence of species is much the same as that when the taxa are ranked according to their number of preopercular sensory canal pores (see p. 119), *viz., Mastacembelus paucispinis* (53 caudal vertebral); the undescribed *Mastacembelus* species (56); *Mastacembelus brachyrhinus* (45); *Mastacembelus crassus* (44); *Mastacembelus brichardi* (42) and *Mastacembelus aviceps* (38). The species having a count of caudal vertebrae below the modal number for African taxa (i.e. about 50) are all characterised by other reductional features.

Moderately small adult size and a deep body are features of all burrowing species (including polychotomy E, and species F to J). These taxa have very elongate, narrow neural and haemal spines compared with those in other species. The relatively long, narrow neural and haemal spines are a synapomorphy of the species complex E, F to J. The moderately small body size in these fishes, relative to that in the majority of mastacembeloids, may be correlated with low vertebral number, and possibly with burrowing habits. An average total count of less than 70 vertebrae was not found in any other mastacembeloids apart from those showing even greater overall reduction in adult size. Thus, in these species (i.e. complex E and F to J) a low vertebral count is treated as a further synapomorphy.

Epicentral and epipleural ribs are a common feature in all mastacembeloids, and are generally present on the 1st to 6th abdominal vertebrae (Travers, 1984: 107). *Mastacembelus sinensis, Chaudhuria* and *Pillaia* are exceptional in that they lack epipleural ribs and have 3 or less epicentral ribs. This low number, relative to the number in all other species is another reductional feature characterising these taxa. Representatives of other perciform assemblages generally have epipleural ribs, the plesiomorphic number being from 4–6. In this respect the majority of mastacembeloids retain the primitive condition, and the absence in *M. sinensis, Chaudhuria* and *Pillaia* is a synapomorphy for these taxa.

Pleural ribs are generally present on all but the first 4 or 5 abdominal vertebrae (Travers, 1984: 107) in mastacembeloids. In some species, including *Mastacembelus brachyrhinus, M. brichardi,* possibly *M. latens, M. crassus* and *M. aviceps* (species O–S in cladogram; Fig. 19) the ribs are confined to the posterior abdominal vertebrae and may only appear on the 20th and subsequent abdominal vertebrae (Travers, 1984: 109). In other eel-like neoteleosts with high abdominal and caudal vertebral numbers, pleural ribs generally appear by the 3rd or 4th abdominal vertebrae. This is the case in the percoid *Cepola rubescens,* the blennioid *Pholidichthys leucotaenia* and the ammodytoid, *Ammodytes tobianus*. Pleural ribs apparently occur on all abdominal vertebrae in synbranchids, but in the congrogadids (e.g. *Congrogadus subduceus*) they are present on only the first 6 abdominal vertebrae. The presence of pleural ribs on the anterior vertebrae appears to be a plesiomorphic condition among percomorph fishes.

The absence, in some mastacembeloids, of pleural ribs from more than the first 4 or 5 abdominal vertebrae is, therefore, an apomorphic condition. The lack of pleural ribs on the first 12 to 20 abdominal vertebrae is a synapomorphic character for *Mastacembelus brachyrhinus, M. brichardi, M. crassus,* and *M. aviceps* (and probably *M. latens*). Five species endemic to Lake Tanganyika also lack pleural ribs on the first 11 to 16 vertebrae. These species are: *Mastacembelus albomaculatus, M. moorii, M. ophidium, M. tanganicae* and *M. micropectus*. Unfortunately, no further characters were found that unite this group or any of its constituent species with the other taxa showing this derived character and the resemblance must be treated as a case of convergence.

DORSAL AND ANAL FIN SPINES

Although the number of dorsal spines varies both inter- and intraspecifically, two groups of species (the *Macrognathus* species, and *Mastacembelus paucispinis* and its undescribed close relative) are distinguished by their comparatively low number of spines.

The low spine numbers in these species have been effected in different ways (see Travers, 1984: 110). In the *Macrognathus* species, the spines are lost from the anterior part of the series but in *Mastacembelus paucispinis* and the new *Mastacembelus* species the spines are lost from the posterior part of the series. The loss of anterior spines is a synapomorphy of the *Macrognathus* species, whilst the posterior loss of spines (associated with an increase in length of the soft-rayed dorsal fin) is a synapomorphy for *Mastacembelus paucispinis* and the undescribed *Mastacembelus* species. The actual number of dorsal spines in *Mastacembelus paucispinis* (7–10) is the lowest found in any spined mastacembeloid examined and is peculiar to this species as are the 15 or 16 found in all specimens of the undescribed species (T. Roberts pers. comm.).

Three anal spines occur in many acanthopterygian fishes (Patterson, 1964; Zehren, 1979). The first 2 are often supported by a single massive pterygiophore connected proximally with the haemal 'cross-bar' of the first caudal vertebra. The third spine is often smaller than the second and may be hidden within a deep skin fold. This arrangement of the anal spines occurs in most perciform assemblages, including the mastacembeloids and is considered to be the plesiomorphic condition.

Among the mastacembeloids there are two exceptions to this arrangement. In *Mastacembelus sinensis* the third anal spine is separated by a distance of 4 vertebrae from the second spine which it equals in size (Travers, 1984: fig. 74), and represents an autapomorphic character of the species. The second exceptional arrangement is the absence of both anal and dorsal spines in *Chaudhuria* and *Pillaia* (Travers, 1984: 109). The absence of fin spines in percomorph fishes is rare (a condition seen for example in some highly aberrant forms such as the schindleroids), and the presence of both anal and dorsal spines among all other mastacembeloids (and the vast majority of percomorph taxa) lends support to the view that the absence of spines in *Chaudhuria* and *Pillaia* must be a character loss associated with the reductional trends manifest in many features of their anatomy.

Intermediate between this condition and the usual one is the presence of two anal spines (supported by a single pterygiophore) in several West African species (e.g. *Mastacembelus batesii, M. brevicauda, M. flavomarginatus, M. greshoffi, M. loennbergii, M. nigromarginatus* and *M. reticulatus*) and two from the Zairean rapids fauna (e.g. *Mastacembelus aviceps* and *M. crassus*). This apomorphic feature may have developed independently or be a synapomorphy for the group. A single anal spine is unique to *M. ophidium* and is an autapomorphic character.

CAUDAL FIN

The arrangement of the caudal skeleton in euteleostean fishes has been summarised by Rosen (1973). Although there is no synapomorphic character uniquely confined to the caudal skeleton of all mastacembeloids, there are significant reductional features which may be used to distinguish major lineages within the group.

The large assemblage recognised as the sister-group to *Mastacembelus sinensis, Chaudhuria* and *Pillaia* can be divided into two groups on the basis of caudal anatomy, namely taxa from SE. Asia and the Middle East (Oriental mastacembeloids), and those from Africa.

Almost all the Asian mastacembeloids (including the Middle Eastern form) have only four hypural elements, an apomorphic condition compared with the six hypurals usual in euteleosteans (Rosen, 1973). The two elements lying below the mid-lateral axis of the vertebral column represent the 1st and 2nd hypurals whilst two dorsal plates represent the upper hypural elements. Faint sutures can often be seen in the upper plates and seem to indicate that they have originated during ontogeny by fusion of separate hypurals present at an early stage of morphogenesis.

Among the Asian (and Middle Eastern) species which otherwise have 4 hypural plates, one species, *Macrognathus aculeatus,* has five elements. As this species is united to other members of this group by a complex of synapomorphic characters (discussed below p. 135) the presence of an extra hypural must be interpreted as the retention of the plesiomorphic condition.

Mastacembelus pancalus (Travers, 1984: fig. 75a) is another exception as it has only a single upper and a single lower hypural plate. This highly derived condition of the hypurals is convergent with that found in some African species (see below).

The presence of 4 hypurals is a synapomorphy of those Asian and Middle Eastern species recognised in the cladogram as two unresolved polychotomies (D & E) and the species complex F to J, this character is evidence in support of the monophyletic origin of this assemblage. The apomorphic hypural number in these mastacembeloids is associated with a number of plesiomorphic caudal characters. These include a relatively high number of principal caudal fin rays (generally 16–18, although there are only 12 in *Mastacembelus pancalus,* and as many as 20 to 21 in *M. keithi* and *M. albomaculatus*); a relatively high number of epurals (e.g. 3 in *Mastacembelus pancalus,* although there are only 2 in *M. unicolor, M. maculatus* and *M. erythrotaenia*); and a distinct caudal fin in several species (although the fin is confluent basally with the dorsal and anal in *Mastacembelus erythrotaenia, M. maculatus, M. caudiocellatus* and *M. circumcinctus*).

All the African taxa show a further development of the trend towards reduction in the caudal skeleton through loss or fusion of hypural elements.

The taxa comprising this group are represented in the cladogram by unresolved polychotomy L, the complex of species K, and species M to S. They are united by a general occurrence in the caudal skeleton of only 2 (occasionally 3, sometimes 1) hypural bones. The 4 hypurals found in a single specimen of *Mastacembelus vanderwaali* are exceptional; an examination of 5 further specimens revealed only 2 separate hypurals to be present in all (Travers, 1984: fig. 76a).

When a total of more than 2 hypural plates is present in species of this group, the additional elements are invariably in the upper part of the fin skeleton, the lower element always remaining a single plate. Two upper hypural plates are present in *Mastacembelus moorii, M. ophidium*, *M. paucispinis* and the undescribed species and, 3 in the one specimen of *M. vanderwaali.* This arrangement in *M. vanderwaali* differs from that in the Asian species whose hypural complement is made up of two upper and two lower elements.

The trend towards hypural fusion among the African species reaches its climax (probably independently) in *Mastacembelus aviceps, M. ellipsifer,* and possibly also in *M. flavidus* and *M. brachyrhinus* (see below). In these species there is a single large hypural plate although its posterior edge is indented slightly in the mid-lateral axis in *M. ellipsifer* and *M. aviceps*, and a faint suture can be detected running from a similar indentation to the base of the hypural plate in *M. flavidus* and *M. brachyrhinus.*

The presence of 2 hypurals (or even a single plate) is a synapomorphy of the African mastacembeloid species, which together with their high numbers of caudal vertebrae, incompletely enclosed scapula foramen, and lack of a urohyal ascending process, is evidence in support of the monophyly of this assemblage. The hypural arrangement in this group is associated with a number of other apomorphic caudal features. These include, a tendency for there to be less than 10 principal caudal fin rays (there are only 4 in some cases e.g. *M. zebratus*), a fused, short, spatulate and non-ray supporting haemal spine on the 2nd preural vertebra, and for the caudal fin to be confluent with the dorsal and anal fins.

The assemblage of Asian species comprising *Mastacembelus sinensis, Chaudhuria* and *Pillaia* (taxa A to C) is recognised as the sister group of all other mastacembeloid assemblages combined (see p. 132). The caudal skeleton in *Mastacembelus sinensis, Chaudhuria* and *Pillaia* is composed of two hypurals (an upper and lower element), a single epural (a uroneural could not be distinguished), the second preural centrum with fused neural and haemal arches that support short spines, confluence of the caudal with the dorsal and anal fins (apart from in *Chaudhuria*, Travers, 1984: 43) and only 8 to 10 principal caudal fin rays. The caudal fin skeleton in this group superficially resembles that in the African taxa since they share the general occurrence of only 2 hypurals, the lack or at most only a single epural, and have neural and haemal arches (with short spines) fused to the 2nd preural vertebra. The African taxa, however, are united by three synapomorphies (the lack of an ascending process on the urohyal or a direct articulation between it and basibranchial I, the scapular foramen not completely bone enclosed, and the tendency for there to be a high ratio of caudal to abdominal vertebrae) which are not found in *M. sinensis, Chaudhuria* or *Pillaia*. Furthermore, all other Oriental mastacembeloids share a synapomorphy (hyomandibula/metapterygoid separation) with the African taxa that is not found in *M. sinensis, Chaudhuria* and *Pillaia*. Thus, the African mastacembeloids share a more recent common ancestry with the larger group of Oriental taxa and because of the numerous synapomorphies shared by *M. sinensis, Chaudhuria* and *Pillaia* (see p. 132 for summary), the caudal fin resemblances between these taxa and the African species are thought to have been independently evolved.

This convergence is most clearly seen in those African species from the lower Zairean rapids (e.g. *M. brachyrhinus, M. brichardi,* possibly *M. latens, M. crassus* and *M. aviceps*; O–S in Fig. 19) and is repeated in several other characters (including features of the orbital and otic regions of the neurocranium p. 110 & 111; the upper jaw p. 113; the ectopterygoid p. 118, and the ventral gill arches p. 121).

SQUAMATION

The mastacembeloids are typically covered in small scales which generally extend over the entire body apart from certain regions of the head. In *Mastacembelus latens* (Roberts & Stewart, 1976), *M. crassus* and *M. aviceps* scales are absent. A total lack of scales is not found in any other taxa apart from *Chaudhuria* and *Pillaia* (Travers, 1984: 115). The loss of scales is but one of many reductional characters found in these taxa. For the reasons discussed above, the nakedness of these African and Asian taxa is considered to have evolved independently and can be added to the list of reductional features occurring convergently in *Chaudhuria, Pillaia,* and species from the lower Zairean fauna.

The presence of scales on only the posterior third of the body in *Mastacembelus micropectus* is a further autapomorphy for this species (see p. 125).

Myology

CEPHALIC MUSCLES

The maxillo-mandibular ligament occurs in most mastacembeloids except several Asian taxa (including *Mastacembelus zebrinus, M. pancalus,* the *Macrognathus* species, and *Mastacembelus sinensis*).

The widespread occurrence of this ligament throughout the teleosts (Winterbottom, 1974) suggests that its loss is an apomorphic reductional feature. It is, therfore a further synapomorphy uniting *Mastacembelus zebrinus, M. pancalus* and *Macrognathus,* which in the absence of any further characters must be considered to have occurred independently (as reductional characters are inclined to do, see p. 110) in *Mastacembelus sinensis.*

A differential development of parts of the *adductor mandibulae* is a myological feature associated with the large rostrum in some mastacembeloids. Part A_2 is generally the dominant part of the adductor complex in teleosts, and the majority of mastacembeloids are no exception. However, in those species with a large rostral appendage part A_1 is greatly enlarged and is the dominant part of the complex (e.g. *Mastacembelus caudiocellatus, M. circumcinctus M. keithi, M. maculatus, M. guentheri* and possibly *M. perakensis* [for which material was unavailable] i.e. polychotomy E, and in *Mastacembelus zebrinus, M. pancalus* and the *Macrognathus* species i.e. F to J in the cladogram). The hypertrophy of part A_1 is probably correlated with its involvement in the movement of the rostral appendage (see Gosline, 1983: 325). However, the mechanism described by Gosline (*op. cit.*) overlooks several other features (discussed below) which also directly control movement of the rostrum.

The tendency for part A_1 to develop as the largest part of the adductor complex is a synapomorphic character of the mastacembeloid group comprising polychotomy E and species F to J.

In *Mastacembelus brachyrhinus, M. brichardi, M. aviceps, M. crassus,* and possibly *M. latens* (i.e. species O–S) the superficial adductor mandibulae musculature (Part A_1 & A_2) has hypertrophied to such an extent that these species are clearly distinguishable from all others. Part A_2 is particularly large and has expanded its site of origin dorsally across the dorsolateral wall and roof of the neurocranium (Travers, 1984: 125). A morphocline involving the extent to which A_2 overlies the dorsal surface of the neurocranium is clearly seen in these species (i.e. O to S). The hypertrophy of part A_2 is a synapomorphy uniting *M. brachyrhinus, M. brichardi, M. crassus* and *M. aviceps* (and probably *M. latens*) and may be related to the reduced eye size in these species, allowing the muscle to expand into the orbit; an arrangement also found in the synbranchids and several microphthalmic catfishes (P. H. Greenwood, pers. comm.). A similar, although less extreme development of the *adductor mandibulae* $A_{1\&2}$ also occurs in two Lake Tanganyikan species (*Mastacembelus albomaculatus* and *Mastacembelus micropectus*) and in *Pillaia,* species which are also characterised by their relatively small eyes.

The *adductor arcus palatini* lies between the ventrolateral wall of the neurocranium and the hyopalatine arch in all mastacembeloids (Travers, 1984: 120); its anterior fibres form the orbital floor. In this form the *adductor arcus palatini* is a characteristic of more advanced teleosts (Winterbottom, 1974: 238). In some taxa e.g. *Mastacembelus caudiocellatus, M. circumcinctus, M. guentheri, M. keithi, M. maculatus* and *M. perakensis* (i.e. all species provisionally placed in the unresolved polychotomy E), and in *Mastacembelus zebrinus, M. pancalus* and the *Macrognathus* species (i.e. species F–J), the anterior fibres extend from the anterolateral face of the parasphenoid across the anterior surface of the ectopterygoid and insert along the attenuated posterior edge of the large first infraorbital bone. This anterior enlargement of the *adductor arcus palatini,* like hypertrophy of A_2, is a synapomorphy of species group E and species F to J.

The enlargement of the anterior region of the *adductor arcus palatini* (like the hypertrophy of the *adductor mandibulae* A_2) is associated with the large rostral appendage in members of taxa E to J. A clear morphocline in the development can be distinguished, beginning with the few fibres that insert on the first infraorbital in *M. keithi* and *M. zebrinus* (Travers, 1984: fig. 88a) and terminating in the broad muscle block virtually separated off from the anterior end of the adductor in *Macrognathus aculeatus* (Travers, 1984: fig. 88b).

The size and degree of independence of the anterior region of the *adductor arcus palatini* is directly correlated with the size of the rostral appendage. The greatest hypertrophy, and the greatest degree of its independence from the main muscle mass, occurs in species with the largest rostral appendage and highest number of rostral toothplates; *M. aculeatus.* Correlated with these changes in the *adductor arcus palatini* is the extent to which the posterior edge of the 1st infraorbital bone is attenuated posterodorsally (Travers, 1984: compare fig. 79b with fig. 86 a, b & c).

Other features of that warrant attention include:

Variation in the form of the rim around the anterior nostril.

The mastacembeloids have both an anterior and a posterior opening to the hypertrophied olfactory sac (p. 107). The posterior nostril is covered by a small flap of skin that can be moved voluntarily in order to open or close it. The anterior nostril lacks a distinct cover, although a number of skin folds lie around the rim. In the majority of species these folds are generally composed of two larger flaps (fimbrules) between which are two narrower ones (fimbriae; see fig. 13a). These flap-like skin folds apparently are used to prevent particles of substrate or debris from entering the anterior nasal opening (Roberts, 1980). In some species the two fimbrules appear to be subdivided, resulting in 6 narrow digitform fimbriae around the rim of the anterior nostril (Fig. 13b). This condition was originally described by Roberts (*op. cit.*) in several Asian mastacembeloids. I have found it (in association with the presence of a relatively large rostral appendage i.e. the apomorphic condition) to occur in *Mastacembelus caudiocellatus, M. circumcinctus, M. guentheri, M. keithi, M. maculatus* and probably *M. perakensis* (species comprising polychotomy E) and *Mastacembelus zebrinus,* *M. pancalus* and the *Macrognathus* species (species F to J in cladogram), and to be a synapomorphy of these taxa. Such an interpretation supports the view originally expressed by Roberts (1980: 390) that, 'This morphological dichotomy ultimately may . . . indicate the derivation of *Macrognathus* from a group of species within *Mastacembelus* that is largely or entirely restricted to Asia'.

II. Intrarelationships of the Mastacembeloidei

The currently recognised intrarelationships of the mastacembeloids as expressed in the present classification of the group (summarised in Fig. 18) cannot be retained since most of the categories are demonstrably non-monophyletic.

Numerous shared derived characters linking taxa at various hierarchical levels strongly suggests that the present delimitation of families and genera is 'unnatural', the result of species being united or separated mainly by the supposed magnitude of their morphological differences and without any attempt to unravel genealogical relationships. For example, at one extreme this practice has resulted in *Pillaia* (and *Garo* see p. 109) being placed in a separate family (Pillaiidae) mainly because of their single upper jaw element, whilst at the other extreme it has resulted in numerous species being lumped in a single genus.

A revision of the intrarelationships of the mastacembeloids based on 77 principle synapomorphies and 27 autapomorphies (several of which occur convergently in some taxa), is outlined in a cladogram (Fig. 19). The cladogram is arranged around 17 nodal points, each of which represents a character or set of characters found in those taxa above the node.

The first node represents a character complex of 18 synapomorphies which are derived features defining the Mastacembeloidei (discussed above p. 108).

The second node represents 10 derived characters (nos. 25–34) and defines one of the two major sister groups into which the mastacembeloids can be divided.

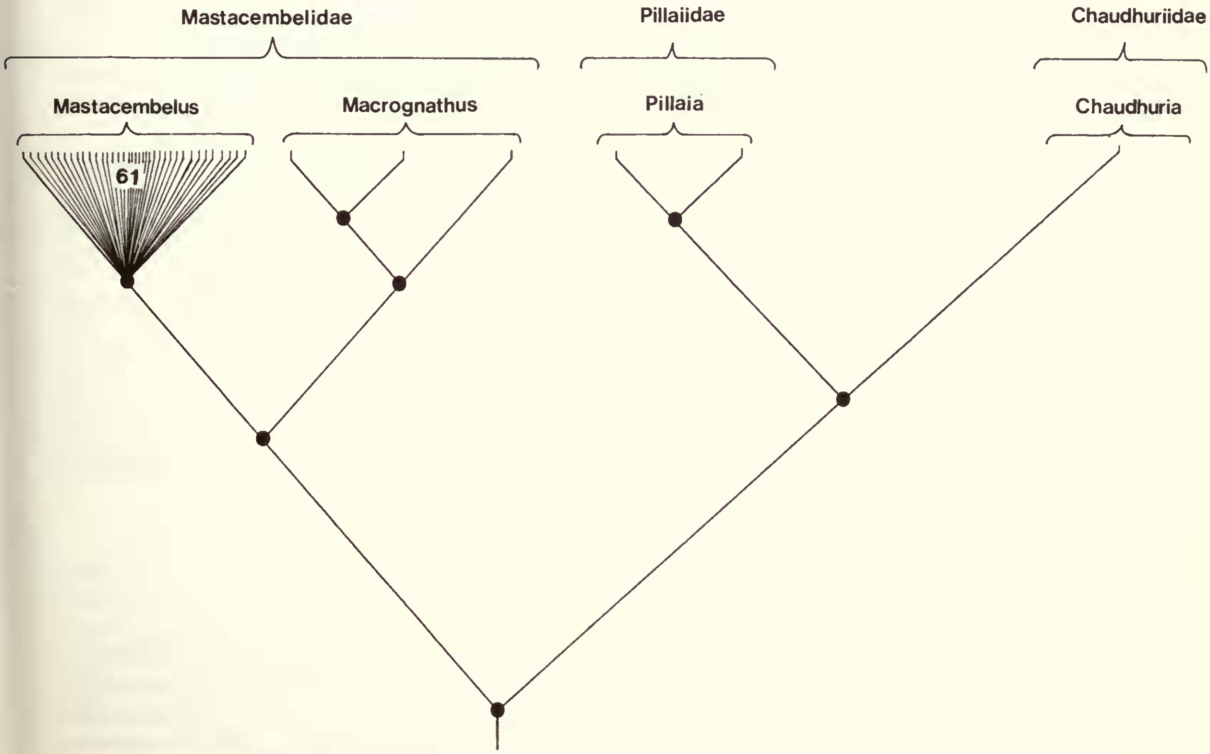

Fig. 18 Relationships of mastacembeloid taxa, as shown by the classification in current use.

These synapomorphies may be summarised as follows:

25. Long narrow posterior parasphenoid processes (p. 111).
26. Dorsomedial processes of the exoccipitals separated by the supraoccipital (p. 112).
27. Dorsal surface of the exoccipital perforated (p. 112).
28. 1–2 inner rows of premaxillary teeth (p. 113).
29. Loss of endopterygoid (p. 116).
30. Ectopterygoid with narrow lateral face (p. 118) and very long anterodorsal process.
31. Palatine reduced in size (p. 118).
32. Interdigitating processes of anterior and posterior ceratohyals reduced or lost (p. 119).
33. Loss of ventral processes on basibranchial 2 (p. 123).
34. Loss of epipleural ribs and 3 or less epicentral ribs (p. 126).

On the basis of these synapomorphies *Mastacembelus sinensis* (species A) is united with *Pillaia* (B, i.e. *P. indica* and presumably *Garo khajuriai* although no material was available for dissection of this species) and *Chaudhuria* (species C, i.e. *C. caudata*) in an assemblage that forms the sister group to all other mastacembeloids.

Although 6 (28, 29, 31, 32, 33 & 34) of the 10 characters defining this lineage are reductional or loss characters that could have arisen independently within the mastacembeloids, they are always found in association with the other 4 characters (25, 26, 27 & 30) that define the taxon. In combination these characters are considered to be reasonable indicators of recent shared common ancestry.

Chaudhuria and *Pillaia* (incorporating *Garo*) share more apomorphic characters than either does with *Mastacembelus sinensis*. The latter species may be defined on the basis of 2 autapomorphies *viz:*

35. Long urohyal dorsal process ascends vertically and tip contacts underside of basibranchial 2 (p. 123).
36. Large 3rd anal spine, equal in size to the 2nd, and separated from it by a distance of 4 vertebrae (p. 127).

The 3rd node in the cladogram represents 14 derived features that link *Chaudhuria* (C) and *Pillaia* (B inclusive of *Garo*) more closely to one another than to any other mastacembeloid. These synapomorphies are:

37. Posterior end of vomerine shaft ventrally depressed (see Travers, 1984: 43 & fig. 15ai & bi).
38. Loss of pterosphenoid (p. 110).
39. Loss of basisphenoid (p. 110).
40. Single foramen in pars jugularis (p. 111).
41. Large saccular bulla lying within the prootic, exoccipital and basioccipital (p. 112).
42. Loss of frontal descending lamina (p. 113).
43. Cephalic sensory canal system reduced or lost (p. 113).
44. Cornomeckelian a small ossicle on medial face of anguloarticular (p. 115).
45. Loss of palatine (p. 116).
46. Ectopterygoid articulation with lateral ethmoid absent, its long anterodorsal arm contacting the vomerine shaft (p. 116).
47. Loss of pharyngobranchial 2 toothplate (p. 124).
48. Loss of dorsal and anal spines (p. 127).
49. Scaleless (p. 129).
50. Extremely small adult size (see Travers, 1984: 32 & 43).

Apart from characters 37 and 46 all these characters are reductional ones (i.e. losses or presumed secondary redevelopments of the plesiomorphic condition). As such they could have arisen independently in more than one lineage. In fact, this is the case with three (39, 40 and 49) which are also found in the highly aberrant African taxa *Mastacembelus crassus* and *Mastacembelus aviceps* (and possibly *M. latens*; taxa Q to S in the cladogram). However, characters of this type are not excluded (see p. 110) and are used because of their congruence with each other as well as with a uniquely derived character (37). This problem is frequently encountered in the analysis of phylogenetic relationships. It is common among systematic studies of perciform lineages (especially the more generalised basal percoids) and has recently been discussed by Johnson (1980: 42) who observed: '. . . the sharing of a number of reductive specialisations in identical states is a reasonable indicator of affinity, even if each character cannot be shown to be uniquely derived'. The problem has also recently been highlighted in characiform studies by Weitzman & Fink (1983: 345). These authors agree with Johnson (*op. cit.*), but draw attention to the need for comparisons between developmental stages in taxa under the influence of what appear to be heterochronic ontogenetic changes, with similar stages in appropriate outgroups.

Three of the characters used to unite *Chaudhuria* and *Pillaia* (41, 44 & 48) would, at least superficially, appear to be the plesiomorphic condition of the feature. In this instance however, the characters are thought to be secondary redevelopments of the plesiomorphic condition (i.e. plesiomorphic mimics) because this is the most parsimonious explanation in view of the many apomorphic characters shared by *Chaudhuria* and *Pillaia* and all other mastacembeloid taxa (see defining characters, p. 108).

Chaudhuria caudata (C) may be defined on the basis of the following 3 apomorphic characters not found in any other mastacembeloids:

51. Ventral edge of dentary divided (p. 114).
52. Dorsal and anal pterygiophores and fin rays absent from the last 6 or 7 caudal vertebrae, associated with a distinct caudal fin (see Travers, 1984: 43 & fig. 23a).
53. Loss of rostral appendage (p.108).

Pillaia indica (B) may be defined on the basis of 4 apomorphies:

54. Loss of prootic anterior process and fused toothplate on hypobranchial 3 (p. 111 & 124).
55. Single upper jaw element (p. 113).
56. Paired neural spines on many abdominal vertebrae, with a wide opening in the dorsolateral face of the neural arch in most caudal vertebrae (see Travers, 1984: 48 & fig. 22).
57. Microphthalmic (p. 111 & 130).

Most of these characters are reductions and losses that could have arisen independently in several of the highly derived African taxa (e.g. species P to S, discussed below).

The 4th node in the cladogram represents a synapomorphy defining the second major group in the basic mastacembeloid dichotomy, *viz:*

58. Hyomandibula and metapterygoid widely separate, and associated with a large symplectic (p. 116).

This feature unites the majority of mastacembeloid taxa (D to S in the cladogram Fig. 19).

The assemblage may be divided into two principal subgroups as indicated by the 5th and 11th nodes in the cladogram.

The 5th node represents a single synapomorphy:

59. 4 separate and autogenous hypurals (p. 127).

This feature defines a group comprising all the Oriental mastacembeloids (D to J in cladogram) except *Mastacembelus sinensis, Chaudhuria* and *Pillaia* (see above), and which forms the sister group to the African mastacembeloids (taxa K to S, united by node 11 in the cladogram).

Two major sublineages are recognised within the species group D to J.

The first sublineage (D) comprises 6 of the 15 Oriental species recognised by Sufi (1956), and is defined by a single synapomorphy, *viz:*

60. Anterior arm of endopterygoid long and lies between the ectopterygoid and lateral ethmoid connection (p. 116).

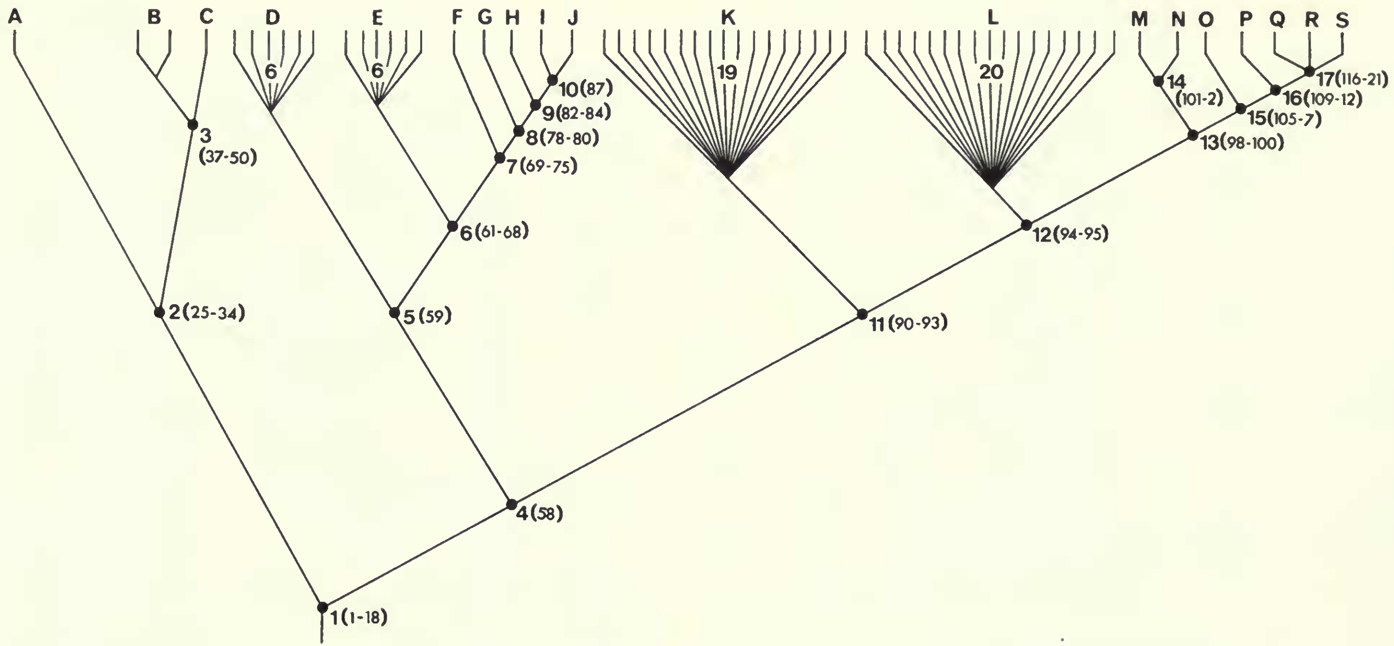

Fig. 19 Cladogram illustrating the proposed phylogenetic intrarelationships of the Mastacembeloidei. Scheme composed of 17 nodes based on principal synapomorphies (given in brackets) listed in text, and autapomorphies and derived characters defining, respectively, individual species (A,C,F,G,H,I,J,M,N,O,P,Q,R and S) and species groups (B,D,E,K, and L). *Key to species and species groups:* A *Mastacembelus sinensis*; B *Pillaia indica* and *Garo khajuriai*; C *Chaudhuria caudata*; D Assemblage of six species (listed on p. 135); E Assemblage of six species (listed on p. 135); F *Mastacembelus zebrinus*; G. *Mastacembelus pancalus*; H *Macrognathus aculeatus*; I *Macrognathus aral*; J *Macrognathus siamensis*; K Unresolved polychotomy (species included listed on p. 137); L Unresolved polychotomy (species included listed on p. 137); M *Mastacembelus paucispinis*; N Undescribed *Mastacembelus* species (Roberts & Travers, in prep); O *Mastacembelus brachyrhinus*; P *Mastacembelus brichardi*; Q *Mastacembelus latens* (provisional, pending further specimens); R *Mastacembelus crassus*; S *Mastacembelus aviceps*.

This character is present in *Mastacembelus armatus, M. erythrotaenia, M. mastacembelus, M. oatesii* and *M. unicolor. Mastacembelus alboguttatus* is tentatively assigned to this group because of its superficial resemblance to the other members, but lack of material precludes a definite decision on its membership.

No other characters were found that make it possible to analyse further the interrelationships of these 6 species which, therefore, are treated as an unresolved polychotomy (D). If polychotomies of this type prove to be inherently unresolvable they could reflect an evolutionary reality (Eldredge & Crancraft, 1980).

The other sublineage stemming from the 5th node (E to J) is defined by 8 synapomorphies, represented by the 6th node in the cladogram, *viz:*

61. Posterior region of parasphenoid undivided, apart from its tip, and excavated to form a pit-like depression on ventral surface (p. 111).
62. Expanded ventrolateral face of exoccipital and posteroventral margin of basioccipital, associated with deep basicranium (p. 111).
63. Deep basioccipital fossa accommodates anterior end of Baudelot's ligament (p.111).
64. Dorsal surface of frontal slopes ventrolaterally (p. 113).
65. Elongate narrow neural and haemal spines, associated with a deep body (p. 126).
66. Relatively low total vertebral count (see p. 126 & Travers, 1984: table 5).
67. Distinct anterior part of *adductor arcus palatini* muscle inserts on the attenuated posterior edge of the 1st infraorbital (p. 130).
68. 6 slender, digitiform fimbriae around rim of each anterior nostril, associated with relatively long rostral appendage (p. 130).

This sublineage contains the remaining 8 *Mastacembelus* species recognised by Sufi (1956) and the 3 *Macrognathus* species recognised by Roberts (1980). It represents a monophyletic assemblage defined by at least 3 unique synapomorphies (61, 67 & 68). Apart from the characters visible without dissection (e.g. 64 & 68), and those visible in radiographs (e.g. 65 & 66), the remaining characters could not be checked in every species because suitable material for dissection was not always available. For that reason *Mastacembelus guentheri, M. keithi* and *M. perakensis* have been placed with *Mastacembelus circumcinctus, M. caudiocellatus* and *M. maculatus* in an unresolved polychotomy (E) pending further research. Detailed studies of *Mastacembelus zebrinus, Mastacembelus pancalus, Macrognathus aculeatus, Macrognathus aral* and *Macrognathus siamensis* however, have revealed a nested series of synapomorphic characters which clearly show the phylogenetic affinity of these species (F to J). The 7th node represents the 7 synapomorphies shared by species F to J, *viz:*

69. Anterolateral expansion of premaxillary tooth-bearing alveolar surface (p. 113).
70. Low and broad coronoid process on dentary associated with tendency for its medial face to the toothed (p. 114).
71. Dorsal edge of anguloarticular with low, broad-based coronoid expansion (p. 115).
72. Indented anterolateral edge of quadrate (p. 116).
73. Tendency for ventral limb of cleithrum to develop a wide lateral face (p. 125).
74. Loss of the maxillo-mandibular ligament (p. 129).
75. Tendency for A_1 to become the largest part of the *adductor mandibulae* muscle, and for tA_1 to be a long, strap-like tendon extending to rostral appendage (p.129).

This suite of characters could be considered as a single transformation as they appear to be closely correlated (i.e. all can be functionally associated with the jaw mechanism) and may result from a common heterochronic ontogenetic shift. *Mastacembelus zebrinus* (species F) shows the suite of synapomorphies represented by the 7th node in the cladogram and is defined by two autapomorphies:

76. Extremely wide ventrolateral face of cleithrum producing 'keeled' pectoral girdle (p. 125).
77. Urohyal ascending process long and thin, its dorsal tip contacting basibranchial 2 and anterior margin connected to the posterior edge of the keel on basibranchial 1 (p. 123).

The 8th node represents 3 synapomorphies that unite *Mastacembelus pancalus* (species G) more closely with the *Macrognathus* species than to any other mastacembeloid.

These characters are:

78. Loss of palatine spur (p. 118).
79. Preopercular sensory canal with 3 central pores at the end of short descending branches (p. 119).
80. Basibranchial 1 keel with a cartilaginous ventral edge and direct articulation with the urohyal (p. 122).

Although characters 79 and 80 are both neomorphs, character 78 is a reductional one and as such could have arisen independently (see p. 118) as it does in *Mastacembelus maculatus*. However, in combination with the two other apomorphic characters it is considered to be a reliable indicator of the close phylogenetic relationship between these species.

Mastacembelus pancalus is defined by a single autapomorphy:

81. Faceted connection between anteromedial margin of quadrate and posterolateral face of ectopterygoid (p. 118).

The 9th node in the cladogram represents 3 synapomorphies that unite the *Macrognathus* species (H to J). These can be summarised as follows:

82. Fragmentation of premaxillary toothbearing alveolar surface into small pairs of plates along ventral surface of the rostral appendage (p. 114).
83. Dorsal edge of anguloarticular notched by facet anterior to posterodorsal corner of the bone (p. 115) and flange on lateral commissure of prootic (p. 112).
84. Low number of dorsal spines resulting from loss of anterior elements in the series (p. 127).

Character 82 is the underlying synapomoprhy of this group and its division into a further 3 separate states (85, 88 & 89) clearly demarcates the *Macrognathus* species each from the other. *Macrognathus aculeatus* (species H) can be defined by the state of the group's synapomorphy, and by a 2nd apomorphic character:

85. Rostral toothplates usually in 38–55 pairs (p. 114).
86. Extremely large basisphenoid, associated with wide opening to posterior myodome (see Travers, 1984: 53 & fig. 30a & b).

The 10th node represents a single synapomorphy which indicates the closer relationship of *M. aral* (species I) and *M. siamensis* (species J) to one another than either is to *Macrognathus aculeatus*.

87. Deeply notched posterolateral margin of pterosphenoid forming anterior region of trigeminal foramen (see Travers, 1984: 65 & fig. 29a).

Macrognathus aral and *Macrognathus siamensis*, respectively, may be defined by the state of the group synapomorphy (i.e. 82) in each species:

88. Rostral toothplates: 14–28 pairs (p. 114).
89. Rostral toothplates: 7–14 pairs (p. 114).

The 11th node represents 4 synapomorphies uniting members of the 2nd branch of the main dichotomy (the 4th node in the cladogram). The synapomorphies uniting this assemblage, which includes all the African taxa but no others, are:

90. Lack of ascending process on urohyal or direct articulation between this bone and basibranchial 1 (p. 122).
91. Hypural plates, generally 2; tendency for parhypural fusion to ventral edge of lower plate; 8–10 principal fin rays and confluent caudal fin (p. 128).
92. Scapula foramen not completely bone enclosed (p. 125).
93. Tendency to have noticeably more caudal than abdominal vertebrae (p. 126).

Within this assemblage, 2 major subdivisions (K, and L to S in the cladogram) can be recognised. Subdivision K serves, for the time being, as a 'catch-all' assemblage for species united by the presence of synapomorphies 90–93. No other characters could be determined which would allow further subdivision of the group which, therefore, is represented as an unresolved polychotomy. Included in this group are *Mastacembelus albomaculatus, M. cunningtoni, M. ellipsifer, M. flavidus, M. frenatus, M. micropectus, M. moorii, M. ophidium, M. plagiostomus, M. platysoma, M. tanganicae, M. zebratus, M. congicus, M. shiranus, M. stappersii* and *M. vanderwaali.* A number of other nominal species (listed in Travers, 1984: table 1), for which material was unavailable should probably also be included.

The second major subdivision (L to S) is represented by the 12th node in the cladogram, and is defined by 2 synapomorphies:

94. No toothplate on pharyngobranchial 2 (p. 124).
95. Less than 5 preopercular sensory canal pores (p. 119).

Both these are loss features, and each has arisen separately, but never in combination (see p. 119 & 124), in several of the species lumped provisionally in species complex K. Since these characters are found in combination only in taxa L to S, they are taken to indicate the phylogenetic unity of the assemblage.

Group L to S (12th node in cladogram) can be subdivided into two sub-groups; L and M to S. L is a polychotomy (discussed on p. 123) of at least 15 species *viz: Mastacembelus batesii, M. brevicauda, M. flavomarginatus, M. goro, M. greshoffi, M. liberiensis, M. loennbergii, M. longicauda, M. marchii, M. marmoratus, M. niger, M. nigromarginatus, M. reticulatus, M. sclateri,* and *M. ubangensis,* and may possibly include several of the species for which study material was unavailable (see Travers, 1984: table 1). The second group contains species M to S, *viz*: *Mastacembelus paucispinis, M. brachyrhinus, M. brichardi, M. latens, M. crassus, M. aviceps* and the undescribed species (see p. 119).

Group L is defined by 2 synapomorphies:

96. Loss of anterior process on hypobranchial 3, and no ligamentous connection to basibranchial 2 (p. 124).
97. Arched ventral processes on basibranchial 2 (p. 123).

Although character 96 is a reductional one it is atypical of the condition in most outgroup taxa and is found in no other mastacembeloids. Therefore, it should be treated as a derived feature. Character 97 is a synapomorphic feature for this lineage. No other characters were found which would enable the interspecific relationships of these species to be resolved further, for the present they remain as an unresolved polychotomy.

This is not the case for the second group of the 12th dichotomy. Taxa in this branch are united by 3 synapomorphies represented by the 13th node, *viz*:

98. A reduction in the number of preopercular sensory canal pores (p. 119).
99. Loss of toothplate on hypobranchial 3 (p. 124).
100. A reduction in the number of caudal vertebrae (p. 126).

Although character 99 mimics the plesiomorphic condition, it is thought to be a secondary reduction that has arisen, independently, in some species recognised as part of polychotomy L (see p. 124). In combination, however, these characters are considered to be a unique synapomorphy suite for the species in which they occur (i.e. M to S).

Detailed analysis of the species in this group has led to the resolution of their interspecific relationships.

The 14th node in the cladogram represents 2 synapomorphies shared by *Mastacembelus paucispinis* and the undescribed *Mastacembelus* species. These are taken as indicative of the taxa being more closely related to one another than either is to any other species. These synapomorphies are:

101. Low number of dorsal spinous rays (their loss occurring posteriorly in the series), combined with a long soft rayed dorsal fin that extends across the junction between abdominal and caudal vertebrae (p. 127).

102. Tendency for the anterior tip of the prootic to form a bridge by contacting the ventral edge of a pedicel on the frontal (p. 111).

Although character 101 is a synapomorphy for both species, it can be separated into 2 states, each of which is species specific. Thus, *Mastacembelus paucispinis* (species M) can be defined by its having:

103. 7–10 dorsal spines (p. 127).

and the undescribed *Mastacembelus* species (N) by its having:

104. 15–16 dorsal spines (p. 127).

The 15th node in the cladogram represents 3 synapomorphies uniting the remaining 5 species, *viz*:

105. Loss of pleural ribs from the anterior abdominal vertebrae (p. 126).
106. Coronomeckelian very short (p. 115).
107. Part A_2 of the *adductor mandibulae* hypertrophied (p. 130).

These taxa can be considered a small species flock as they are endemic to the highly specialised rapids environment of the Lower Zaire River and conform to the prerequisite criteria discussed by Greenwood (1984). Of their features, 105 is a reductional one which does occur in some species provisionally assigned to species complex K (see p. 126). Whether this indicates that it has occurred independently in these various taxa or whether it indicates that the species in K may eventually be included in this group (O to S), cannot be determined at present.

Mastacembelus brachyrhinus (species O) may be distinguished from other species associated through node 15 by a single autapomorphic feature:

108. Dorsal expansion of the pterotic, associated with relatively small parietals, posterior expansion of frontals, and a tendency for the extrascapulae to be independent (p. 97).

The 16th node represents the following 4 synapomorphies:

109. Relatively large saccular bulla (accommodated entirely within the prootic, see p. 112).
110. Short anterior region of frontal; roofs small orbital cavity (see p. 113).
111. Endopterygoid very small and splinter-like (see p. 116).
112. Ventral limb of cleithrum short and indistinct (p. 125).
113. Tendency to be microphthalmic or cryptophthalmic (p. 113 & 130).

These synapomorphies unite *Mastacembelus brichardi* (species P), *Mastacembelus crassus* (species R) and *Mastacembelus aviceps* (species S), and probably *Mastacembelus latens* (species Q) as well, although lack of material precludes a definite allocation of this species. *Mastacembelus brichardi* may be distinguished from the other species by 2 autapomorphies, *viz:*

114. Loss of pigment (p. 85).
115. Eyes extremely small and lying medial to the *levator arcus palatini* muscle (see Travers, 1984: 125 & fig. 84b).

The remaining taxa in the lineage containing species M to S are *Mastacembelus crassus* (R), *M. aviceps* (S) and, probably, *M. latens* (Q).

The 17th node in the cladogram represents 6 synapomorphies for these species, *viz*:

116. Scaleless (p. 129).
117. Loss of basisphenoid (p. 110).
118. Anterior process of prootic very short or absent (p. 111).
119. Ectopterygoid with narrow anterolateral face (p. 118).

120. Dorsal opening of preopercular sensory canal on the posterior edge of preoperculum (p. 119).
121. Low 'keel' on basibranchial 1 (p. 121).

Mastacembelus latens is provisionally included in this group on the grounds that it shares one of these apomorphic characters (116). Until specimens of *M. latens* are available for dissection, the presence or absence of the other 5 synapomorphies cannot be determined.

The 6 synapomorphies shared by *Mastacembelus crassus* and *Mastacembelus aviceps* (and possibly *M. latens*) are all reductional ones. Several of these characters (all, apart from 120 & 121), or at least the tendency for their manifestation, are seen in *Pillaia* and in *Chaudhuria* (to a lesser extent). However, these taxa are clearly more closely related to *Mastacembelus sinensis* (as discussed on p. 128) and this complex of 6 characters in combination is an indicator of the close phyletic affinity of *M. crassus* and *M. aviceps*.

Mastacembelus crassus (species R) can be distinguished from *Mastacembelus aviceps* (S) by a single apomorphic character, *viz*:

122. Tendency for the trigeminal and facial foramina to be confluent (p. 111).

Whereas, *M. aviceps* can be identified by a combination of 5 apomorphic features, of which three are autapomorphic (i.e. 123, 124 & 125), *viz*:

123. Extremely small, splinter-like pterosphenoid lying along dorsolateral edge of frontal (p. 110).
124. Loss of neurocranial precommissural lateral wall and trigeminofacialis foramina (Travers, 1984: 68 & fig. 40a & b).
125. Anterior region of maxilla reduced to a weak and thin process tightly connected to premaxilla (p. 113).
126. Loss of ventral processes on basibranchial 2 (p. 123).
127. Hypurals fused into single fan-like plate (p. 128).

These characters, and that defining *M. crassus* are all reductional ones; one of them (character 127) also occurs in *Mastacembelus ellipsifer* (see p. 128), and is a further example of a reductional feature developing independently.

Proposed changes in classification

Comparison of the present state of mastacembeloid taxonomy (Fig. 18) with the phylogeny of the group (Fig. 20) reveals the necessity for numerous alterations to the existing classification, if the phylogenetic relationships of the species are to be reflected. These taxonomic and nomenclatural changes can be summarised as follows:

Re-allocation of the Mastacembeloidei from the Perciformes to the Synbranchiformes, as a sister taxon of the Synbranchoidei.

Expansion of the family Chaudhuriidae to incorporate two genera.

Elevation of *Mastacembelus sinensis* to a monotypic genus of the Chaudhuriidae.

The generic synonymy of *Chaudhuria* with *Pillaia* (and *Garo* see p. 109), but retention of both taxa as subgenera of *Chaudhuria*.

Division of the Mastacembelidae into two subfamilies (representing the Asian and African species, respectively).

Restriction of the *Mastacembelus* generic concept to five Asian and one Middle Eastern species only.

Expansion of the *Macrognathus* generic concept to include eight Asian species previously included in *Mastacembelus*.

Creation of a new subfamily for the African taxa.

Creation of new genera for the major African sublineages.

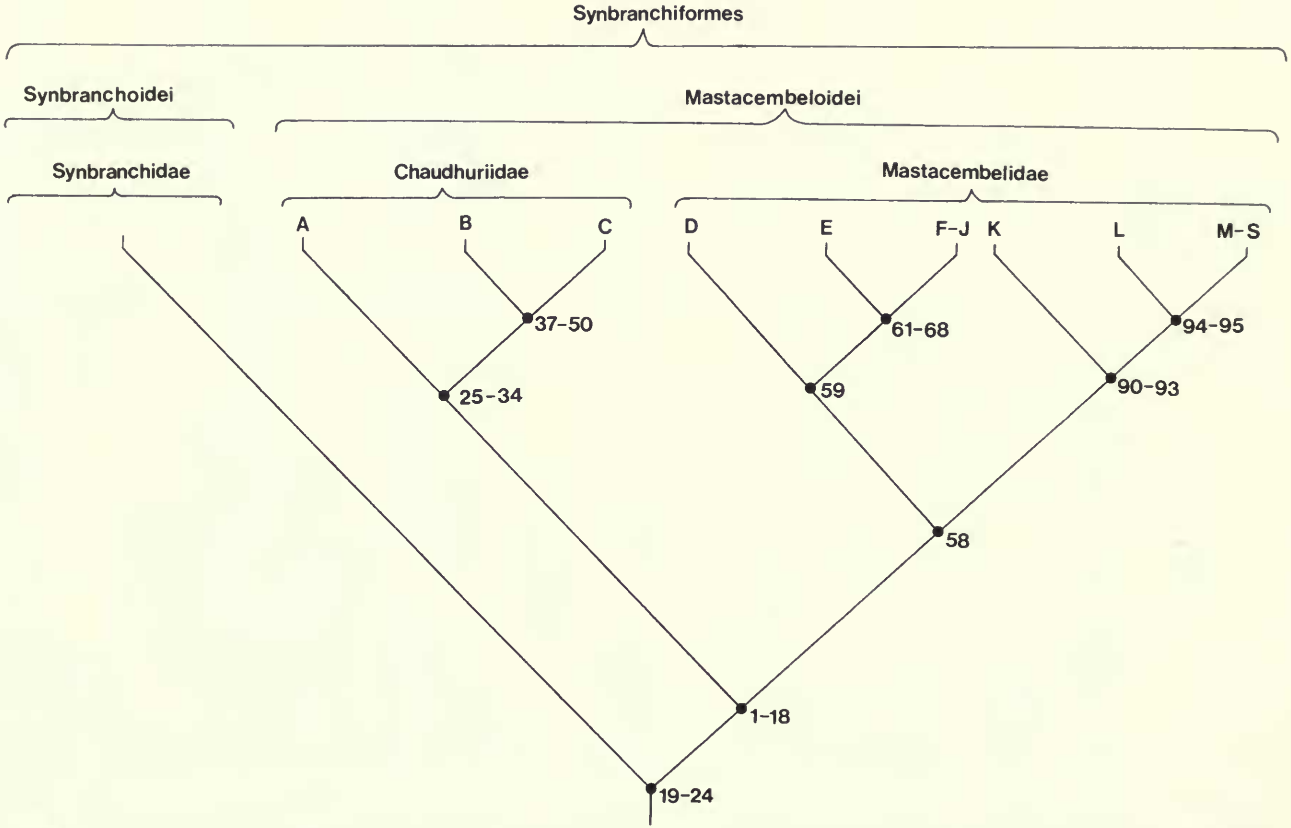

Fig. 20 Phylogeny of the Mastacembeloidei. Principal synapomorphies (given as a number) on which each node is based, and derived characters defining each of the terminal taxa A–S, are given in the text.

Diagnoses for the Synbranchiformes, its suborders, families, subfamilies and genera

Order **SYNBRANCHIFORMES** Berg 1940

Berg, L. S., 1940. Classification of fishes, both recent and fossil. *Trav. Inst. Zool. Acad. Sci. U.S.S.R.* **5:** 1–517, (English translation).

Diagnosis. Eel-shaped acanthomorph fishes of small to moderate size (attaining max. length of approx. 1 m). Burrowing and cavernicolous habit commonly displayed. Lack pelvic fins or girdle, with caudal fin reduced or absent. Gill membrane attached to lateral wall of body by expansion of *hyohyoidei adductores* muscle; restricted opercular opening and insertion of *levator operculi* on lateral face of operculum. Prominent *adductor mandibulae* musculature, with part A_1 lying ventral to A_2, the latter tending to encroach across dorsal surface of neurocranium and into orbital cavity. Eyes small and well forward in skull. Anterior and posterior nostrils. Cycloid scales, small and oval, sometimes absent. Neurocranium attenuated, particularly precommissural region involving frontals, pterospenoid, vomer and parasphenoid; dorsal surface lacks crests or any form of sculpturing. Frontals turned down with prominent descending lamina. Infraorbital bones reduced apart from 1st. Palatines joined firmly to vomer in midline; generally tooth bearing. Vomer a long thin strut. Ectopterygoid articulates with lateral ethmoid, vomer or both. Non-protrusile upper jaw. Maxilla and premaxilla long and strut-like, with symphyseal and articulatory processes reduced or absent. Dentary with posterior extension along ventral edge of anguloarticular. Pectoral girdle remote from basicranium, posttemporal bone reduced (accompanied by loss of connection to pectoral girdle) or lost. Flexible craniovertebral joint. Dorsal gill arch skeleton positioned posteriorly; lacks first pharyngobranchial bone, with second pharyngobranchial reduced or absent. Numerous vertebrae.

Pantropical and subtropical fishes from freshwaters at high and low elevations; some individuals reported from brackish waters; tendency for facultative air breathing and sex reversal. 83 extant species currently recognised (no fossil record) in two suborders.

Suborder **SYNBRANCHOIDEI** Boulenger, 1904

Boulenger, G. A., 1904. A synopsis of the suborders and families of teleostean fishes. *Ann. Mag. nat. Hist.* (7), **13:** 161–190.

Diagnosis. Monotypic suborder with synbranchiform features given above. For annotated account of groups, species diagnoses and key see Rosen & Greenwood (1976: 49–66).

Suborder **MASTACEMBELOIDEI** Greenwood *et al,* 1966

Greenwood, P. H., Rosen, D. E., Weitzman, S. H. & Myers, G. S. 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms.
Bull. Am. Mus. nat. Hist. **131:** 339–456.

OPISTHOMI Boulenger, G. A., 1904. *Ann. Mag. nat. Hist.* (7), **13:** 161–190. (subordinal rank).
Regan, C. T., 1912. *Ann. Mag. nat. Hist.* (8), **9:** 217–219 (ordinal rank).
MASTACEMBELIFORMES Berg, L. S., 1940. *Trav. Inst. Zool. Acad. Sci. U.S.S.R.* **5:** 1–517.

Diagnosis. Synbranchiform fishes with long dorsal and anal fin composed of isolated spinous rays anterior to long series of soft branched rays. Rostral appendage formed from anterior nostrils (at end of tubular extensions) positioned lateral to a central rostral tentacle. Rim of anterior nostril generally with two wide (fimbrules) and two narrow (fimbriae) flaps of skin. '*Musculus intraoperculi*' differentiated within opercular series. Elongate ethmovomerine region with long nasal and 1st infraorbital bones. Preorbital spine (posterior tip of 1st infraorbital) generally pierces skin. Tubular lateral ethmoids accommodate anterior end of massive *nervus olfactorius.* Pterosphenoids, joined firmly in midline; frontals completely enclose foramen magnum. Small compressed basisphenoid, occasionally absent. Anterior regions of prootic and sphenotic attenuated; former having long process extending into orbital cavity and latter having wide lateral flange. Saccular bulla generally small and house entirely within the prootic. Extrascapulae (lateral and medial) lost and sensory canal enclosed by parietal. 'Ball and socket' craniovertebral joint. *Obliquus superioris* with anterior insertion on posterior edge of exoccipital. Posterior end of Baudelot's ligament forked. Very large coronomeckelian dorsal to dentary, across lateral face of suspensorium. Pair of ventral processes on basibranchial 2. Hypobranchial 3 with a round toothplate fused to dorsal surface. Pseudobranch present.

Ethiopian and Oriental distribution. Wide range in tropical and subtropical Africa, and in Asia continuously from Middle East to islands of Indonesia, and eastern China seaboard. 68 species currently recognised, in two families.

Family **CHAUDHURIIDAE** Annendale, 1918

Annendale, N., 1918. Fish and fisheries of the Inle Lake. *Rec. Ind. Mus.* **14:** 33–64.

TYPE GENUS. *Chaudhuria* Annendale, 1918.

DIAGNOSIS. Derived mastacembeloid fishes with above features but tending to small adult size and reduction or loss of many characters by heterocrony. Rostral appendage reduced or lost. Needle-like parasphenoid posterior processes. Dorsomedial region of exoccipital with perforated dorsal surface and separated from opposite number. 1–2 inner rows of premaxillary teeth. Ectopterygoid with narrow lateral face and very long antero-dorsal process. Palatine reduced in size (lacks suborbital flange). Three or fewer epicentral ribs. Interdigitating processes of anterior and posterior ceratohyals reduced or lost. No endopterygoid, basibranchial 2 ventral processes or epipleural ribs.

Confined to China (including Taiwan and possibly Korea), Thailand, Burma and northern India. Family expanded to incorporate 4 species in two genera.

Genus ***RHYNCHOBDELLA*** Bloch & Schneider, 1801

Blotch, M. E. & Schneider, J. G., 1801. M. E. Blochii Systema Ichthyologiae iconibus ex illustratum. Post oblitum auctoris opus inchoatum absolvit, correxit, interpolavit . . . J. G. Schneider, Saxo. Berolini.

TYPE SPECIES. *Rhynchobdella sinensis* Bleeker, 1870

DIAGNOSIS. Monotypic chaudhuriid genus. Parietals may contact medially; very large 3rd anal spine equal in size to the 2nd spine and separated from it by four vertebrae. Tip of vertical urohyal ascending process contacts underside of basibranchial 2.

Widely distributed in China, Taiwan and possibly N. & S. Korea.

Genus ***CHAUDHURIA*** Annendale, 1918

Annendale, N., 1918. Fish and fisheries of the Inle Lake. *Rec. Ind. Mus.* **14:** 33–64.
Pillaia Yazdani, G. M., 1972. *J. Bombay Nat. Hist. Soc.* **69**(1): 134–135; Talwar, P. M., Yazdani, G. M. & Kundu, D. K., 1977. *Proc. Indian Acad. Sci.* **85:** 53–6.
Garo Yazdani, G. M. & Talwar, P. M., 1981. *Bull. zool. Surv. India* **4**(3): 287–288.

TYPE SPECIES. *Chaudhuria caudata* Annendale, 1918

DIAGNOSIS. Highly derived chaudhuriid fishes with particularly small adult size (generally between 40–60 mm.). Extreme reduction of many features appears to mimic plesiomorphic condition e.g. large saccular bulla partly within prootic, exoccipital and basioccipital, coronomeckelian reduced to a small ossicle on medial face of anguloarticular. Loss of numerous features including; pterosphenoid, basisphenoid, frontal ventral lamina, cephalic sensory canal system (reduced or lost), palatine, pharyngobranchial 2 toothplate, dorsal and anal spines, and scales. Lack of ectopterygoid articulation with lateral ethmoid (ectopterygoid directly contacts lateral face of vomerine shaft); possibly associated with loss of palatine. Posterior end of vomer ventrally depressed; pars jugularis pierced by single relatively large foramen.

Three species confined to Thailand, Burma and northern India:
Chaudhuria caudata Annendale, 1918
Chaudhuria indica (Yazdani), 1972
Chaudhuria khajuriai (Talwar, Yazdani & Kundu), 1977.

Family **MASTACEMBELIDAE** Günther, 1861

Günther, A., 1861. Catalogue of the acanthopterygian fishes. **3.** London.

TYPE GENUS. *Mastacembelus* Scopoli, 1777

DIAGNOSIS. Mastacembeloid fishes with features as for the suborder (given above) and, additionally: wide separation of hyomandibula and metapterygoid, associated with large symplectic.

64 species widespread throughout the range of the suborder. Two subfamilies comprise the mastacembeloids Oriental and Ethiopian regions.

Subfamily **MASTACEMBELINAE** subfam. nov.

TYPE GENUS. *Mastacembelus* Scopoli, 1777

DIAGNOSIS. Mastacembelid fishes with distinct caudal fin generally unconnected to posterior ray of dorsal or anal fin. If connected (by membrane) caudal fin rays extend posterior to, and remain distinct from, last posterior dorsal and anal fin ray. Caudal fin skeleton with 4 separate and autogenous hypural plates. Rostral appendage varies from very large to intermediate size. Tendency to be brightly coloured.

17 species widely distributed from Middle East to SE. Asia including China and continental islands of Indonesia, arranged in two genera.

Genus ***MASTACEMBELUS*** Scopoli, 1777

Scopoli, J. A., 1777. Introductio ad Historiam Naturalem, Prague.

TYPE SPECIES. *Mastacembelus mastacembelus* (Banks & Solander, in Russell), 1794; See Wheeler, 1955.

DIAGNOSIS: Mastacembeline fishes of moderate to large size (over 50 cm.). Attenuated anterior arm of endopterygoid lies between ectopterygoid and lateral ethmoid connection. Neurocranium broad with rostral appendage of moderate size.

6 species, five widely distributed in SE. Asia including the continental islands of Indonesia:
Mastacembelus alboguttatus Boulenger, 1893
Mastacembelus armatus (Lacépède), 1800
Mastacembelus erythrotaenia Bleeker, 1870
Mastacembelus oatesii Boulenger, 1893
Mastacembelus unicolor (Kuhl & van Hasselt) Cuv. & Val., 1831

and the single Middle Eastern species:
Mastacembelus mastacembelus (Banks & Solander, *in* Russell), 1794.

Genus ***MACROGNATHUS*** Lacépède, 1800

Lacépède, B., 1800. *Histoire naturelle des poissons.* Paris 2.

TYPE SPECIES. *Ophidium aculeatum* Bloch, 1786

DIAGNOSIS. Mastacembeline fishes of moderate to small size (under 50 cm.). Deep bodied with elongate, narrow neural and haemal spines. Rostral appendage large and more elongate than in other mastacembeloids. Six slender and digitiform fimbriae surround rim of each anterior nostril. Distinct anterior part of *adductor arcus palatini* muscle inserts on attenuate posterior edge of 1st infraorbital. Narrow, but deep, neurocranium with dorsal surface of frontals sloping ventrally; ventrolateral face of exoccipital and posteroventral margin of basioccipital expanded. Posterior region of parasphenoid undivided (apart from tip) and excavated to form pit-like depression on ventral surface of basicranium (for muscle attachment). Deep basioccipital fossa accommodates anterior end of Baudelot's ligament. Vertebral count relatively low. In addition, see diagnosis given by Roberts (1980: 387). Roberts' (1980) *Macrognathus* generic concept (i.e. *Macrognathus aculeatus, M. aral* and *M. siamensis*) now expanded to include eight Oriental species previously assigned to *Mastacembelus* (i.e. *'Mastacembelus' caudiocellatus, 'M'. circumcinctus, 'M'. guentheri, 'M'. keithi, 'M'. maculatus, 'M'. pancalus, 'M'. perakensis* and *'M'. zebrinus*).

11 species widely distributed in SE. Asia and continental islands of Indonesia:

Macrognathus aculeatus (Bloch), 1786
Macrognathus aral (Bloch & Schneider), 1801; see Roberts, 1980
Macrognathus siamensis (Günther), 1861; see Roberts, 1980
Macrognathus caudiocellatus (Boulenger), 1892
Macrognathus circumcinctus (Hora), 1924
Macrognathus guentheri (Day), 1865
Macrognathus keithi (Herre), 1940
Macrognathus maculatus (Cuv. & Val.), 1831
Macrognathus pancalus Hamilton Buchanan, 1822
Macrognathus perakensis (Herre & Myers), 1937
Macrognathus zebrinus (Blyth), 1859

Subfamily **AFROMASTACEMBELINAE** subfam. nov.

TYPE GENUS. *Afromastacembelus* gen. nov.

DIAGNOSIS. Mastacembelid fishes with confluent caudal fin rays continues with posterior rays of dorsal and anal fin. Caudal fin skeleton generally with two separate and autogenous hypurals, tend to have parhypural fused to lower edge of ventral element and to have only 8–10 principal fin rays. Loss of ascending process on urohyal and direct articulation between urohyal and basibranchial 1. Scapula foramen not completely bone enclosed. Tendency to have noticeably more caudal than abdominal vertebrae.

This subfamily represents the Ethiopian mastacembelid species widely distributed throughout tropical and subtropical regions of the continent. 46 species currently recognised and provisionally arranged in two genera.

Genus ***CAECOMASTACEMBELUS*** Poll, 1958

Poll, M., 1958. Description d'un poisson aveugle nouveau du Congo Belge appartenant à la famille des Mastacembelidae. *Revue Zool. Bot. Afr.* **57**: 388–392.

TYPE SPECIES. *Caecomastacembelus brichardi* Poll, 1958

DIAGNOSIS. Afromastacembeline fishes of small to moderately large size. With no pharyngobranchial 2 toothplate and less than five preopercular sensory canal pores. Species with atrophied eye tissues and one (i.e. type for genus) is anoptic. General morphological simplification (by secondary reduction and loss) occurs in microphthalmic and cryptophthalmic species (parallels condition in *Chaudhuria,* although not carried to such extremes).

Distributed predominently in western half of continent and includes small species flock endemic to lower Zairean rapids. At least 22 species tentatively assigned to this genus, and probably several more, for which study material was unavailable (see Travers, 1984: table 1):

Caecomastacembelus aviceps (Roberts & Stewart), 1976
Caecomastacembelus batesii (Boulenger), 1911
Caecomastacembelus brachyrhinus (Boulenger), 1899
Caecomastacembelus brevicauda (Boulenger), 1911
Caecomastacembelus brichardi Poll, 1958

Caecomastacembelus crassus (Roberts & Stewart), 1976
Caecomastacembelus flavomarginatus (Boulenger), 1898
Caecomastacembelus goro (Boulenger), 1902
Caecomastacembelus greshoffi (Boulenger), 1901
Caecomastacembelus latens (Roberts & Stewart), 1976
Caecomastacembelus liberiensis (Steindachner), 1894
Caecomastacembelus loennbergii (Lönnberg), 1895
Caecomastacembelus longicauda (Boulenger), 1907
Caecomastacembelus marchii (Sauvage), 1892
Caecomastacembelus marmoratus (Perugia), 1892
Caecomastacembelus niger (Sauvage), 1878
Caecomastacembelus nigromarginatus (Boulenger), 1898
Caecomostacembelus paucispinis (Boulenger), 1899
Caecomastacembelus reticulatus (Boulenger), 1911
Caecomastacembelus sclateri (Boulenger), 1903
Caecomastacembelus ubangensis (Boulenger), 1911
Caecomastacembelus sp.

and probably:

Caecomastacembelus ansorgii (Boulenger), 1905
Caecomastacembelus cryptacanthus (Günther), 1867
Caecomastacembelus laticauda (Ahl), 1937
Caecomastacembelus sanagali (Thys van den Audenaerde), 1972
Caecomastacembelus seiteri (Thys van den Audenaerde), 1972

Genus ***AFROMASTACEMBELUS*** gen. nov.

TYPE SPECIES. *Mastacembelus tanganicae* Günther, 1893

DIAGNOSIS. Afromastacembeline fishes of moderate to large size; occur predominently from eastern half of continent and include species endemic to Lake Tanganyika. All afromastacembeline species, other than those assigned to *Caecomastacembelus,* provisionally lumped in this 'catch-all' assemblage (which may not be monophyletic) pending closer examination of groups interspecific relationships.

At least 16 species tentatively placed in this genus, and probably several more, for which study material was unavailable (see Travers 1984: table 1).

Afromastacembelus albomaculatus (Poll), 1953
Afromastacembelus congicus (Boulenger), 1896
Afromastacembelus cunningtoni (Boulenger), 1906
Afromastacembelus ellipsifer (Boulenger), 1899
Afromastacembelus flavidus (Matthes), 1962
Afromastacembelus frenatus (Boulenger), 1901
Afromastacembelus micropectus (Matthes), 1962
Afromastacembelus moorii (Boulenger), 1898
Afromastacembelus ophidium (Günther), 1893
Afromastacembelus plagiostomus (Matthes), 1962
Afromastacembelus platysoma (Poll & Matthes), 1962
Afromastacembelus shiranus (Günther), 1896
Afromastacembelus stappersii (Boulenger), 1914
Afromastacembelus tanganicae (Günther), 1893
Afromastacembelus vanderwaali (Skelton), 1976
Afromastacembelus zebratus (Matthes), 1962

and probably:

Afromastacembelus moeruensis (Boulenger), 1914
Afromastacembelus signatus (Boulenger), 1905
Afromastacembelus trispinosus (Steindachner), 1911

The revised classification can be summarised as follows:
Series: Percomorpha (consists of 12 orders)
Order: Synbranchiformes
  Suborder: Synbranchoidei
    Family: Synbranchidae (see Rosen & Greenwood, 1976)
  Suborder: Mastacembeloidei
    Family: Chaudhuriidae
          Rhynchobdella
          Chaudhuria
    Family: Mastacembelidae
      Subfamily: Mastacembelinae
            Mastacembelus
            Macrognathus
      Subfamily: Afromastacembelinae
            Caecomastacembelus
            Afromastacembelus

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